Stability of ecological communities with antagonistic interactions

by

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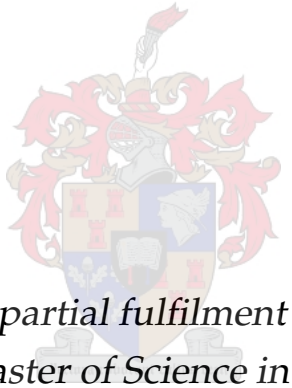

Thesis presented in partial fulfilment of the requirements for the degree of Master of Science in Mathematics in the Faculty of Science at Stellenbosch University

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Co-supervisor: Dr. Pietro Landi

March 2020

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Abstract

Stability of ecological communities with antagonistic interactions

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Stability of large ecological systems has been a focus of theoretical ecology for more than 40 years. Here I review the stability criteria for large communities with antagonistic interactions. I show how dispersal can affect the stability of these interactions using eigenvalues distribution in the complex plane. I further consider a more realistic model, in particular, the logistic population growth with Holling type II functional response and their effect on community stability. I conclude by enumerating basic dynamical characteristics whose properties bring a clear understanding on how stability of large antagonistic ecological networks can be improved. My results highlight that dispersal and density dependence are stabilising while Holling type II functional response is destabilising.

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First and foremost I thank the almighty God for every second on this earth. I would like to express the deepest appreciation to my supervisor, Prof Cang Hui who has given me the opportunity to study masters. Without his guidance help this thesis would not have been possible. I would like to thank Dr Pietro Landi for co-supervision and Dr Guillaume Latombe for the assistance leading to the writing of this thesis. I also would like to thank The Family of Anthony Ball for funding my studies. Special thanks to Dr Pietro Landi for assistance and guidance of thesis. Lastly, I'm thankful to my family for the love and support throughout my academic journey.

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Chapter 1

Introduction

1.1 Background

An ecosystem is a community of living organisms and their interactions with their non-living environment. A community consists of all the populations of all the species that live together in a particular area. The difference between ecosystem and community is that an ecosystem includes the physical structure, while a community does not [2]. The stability of an ecosystem refers to the capability of a natural system to apply self-regulating mechanisms to return to a steady state after disturbance [3]. The equilibrium is the steady state of an ecosystem. An ecosystem may be knocked out of equilibrium by disturbance or disruptive events that affect their composition. This disturbance can be caused by natural processes such as fire or human activities such as deforestration, acid rainfall, and the introduction of invasive species. Different ecosystems may respond differently to the same disturbance. One may recover rapidly, and another may recover more slowly or not at all [2].

An ecosystem's responce to disturbance can be described by two parameters, ie, resistance and resilience. Resistance is the ability of an ecosystem to remain at equilibrium in spite of disturbance while resilience refers to how readily an ecosystem returns to equilibrium after being disturbed [4]. Both resistance and resilience are crucial when considering the effects of disturbances. A severe enough disturbance may change an ecosystem beyond the point of recovery. This could lead to a permanent change or loss of the

ecosystem. So, understanding the impact of our actions on nature is crucial as it affects our lives in numerous ways [5]. These could be financial such as, biomass harvested without driving a population to extinction, or ethical such as, measures taken to ensure biodiversity (ie, the variability among living organisms from all sources of ecosystems) is preserved for future generations [5].

Theoretical research has explored how numerous features of the ecosystem affect stability, including diversity (ie, the number of species), the strength of interactions between species, the topology of those interactions, and the sensitivities of species to different types of environmental disturbances [6]. Biodiversity increases the stability of ecosystem processes in a changing environment, but the mechanisms that underlie this effect are still controversial and poorly understood [7]. One challenging aspect of stability is its many components, including asymptotic stability, resilience, resistance, robustness, persistence and variability [8].

Before the 1970s, ecologists believed that more diverse communities enhance ecosystem stability. Then, Elton [9] argued that "simple communities were more easily upset than that of richer ones, ie, more subject to destructive oscillations in populations, and more vulnerable to invasions". These intuitive ideas were challenged by the work of Robert May in 1972 [10] who exposed a seemingly fundamental contradiction between encountered ecological intuition adopted by MarArcthur (1955) and Elton (1958) [9]. May turned to mathematics to explore the diversity-stability relationship [11]. Using the linear stability analysis on models constructed from the statistical universe, he found that the number of species destabilise community dynamics [1, 10–15].

Since May's seminal paper, the complexity-stability debate became one of the highly researched topic in community ecology. Many researchers have been motivated to seek ecological and biological mechanisms contributing to the stability of complex communities [16]. However, May's formulation is criticised for three widely different reasons [9]:

1. Populations are not thought to be at equilibrium.

2. Belief persists that if populations are found around equilibrium, these models are not realistic, omitting details of autecology (ie, the ecological study of a particular species) that are important to understand population dynamics.

3. Stability is evaluated with respect to arbitrarily small disturbances.

Recently, the work of May was revisited by Allesina and Tang [12] who established stability criteria for systems where species interact via either mutualism, competition, and predation. Their contribution is a clarification of May's approach that considered mixtures of interaction types. Having derived the stability criteria, Allesina and Tang [14] wanted to assess the effect of imposing a realistic food web structure (see section 1.1.1) within the predator-prey case since it is believed that realistic food web structures should improve stability. Allesina and Tang [14] used their criteria to prove that stability probability for predator-prey networks decreases when a more realistic food web structure is imposed or if there is a large predominance of weak interactions.

Gravel et al. [1] also expanded the approach taken by May to investigate stability looking at the Jacobian matrix of the metaecosystem (ie, different ecosystems connected via dispersal) when placed in a spatial context (see section 1.1.2 and Figure 1.1). Jacobian matrices are obtained by linearising the dynamical system that describes all the species in metaecosystem at equilibrium. They tried to understand how spatial flows among local ecosystems might stabilise dynamics at the metaecosystem scale by considering the technique of local stability analysis, along with random interaction matrices. In their studies, Gravel et al. [1] found that stability criteria are relaxed in direct proportion to the number of ecologically distinct patches in the metaecosystem. Furthermore, they found that the stabilising effect of dispersal (ie, the movement of individuals from one location to another) is maximal at intermediate intensity [1].

1.1.1 Food webs

Food webs are descriptions of who eats whom in an ecosystem [17]. A food web is usually known in ecology as a system of interlocking and interde-

pendent food chains. A food chain is a linear network in a food web starting from producer organisms (such as trees which use radiation from the sun to produce organic nutrients) ending at apex predator species (such as bears or killer whales), detritivores (such as earthworms), or decomposer species (such as bacteria or fungi) [18, 19]. Food webs are part of the key building blocks to describe the interaction of species [5]. Ecological definitions of food web can be in distinct ways, such as the networks formed by trophic interactions among a community or where species are grouped by thier functions into trophic species [20, 21].

Simple food web models have been used for about a century, pioneered by Alfred Lotka and Vito Volterra. They independently derived an identical model of predator-prey interaction [5]. Food webs have no inherent spatial component in their description, but in nature most species participate in some form of movement to gather food, shelter or to find new living space and so on [5]. Food web models, such as the cascade and niche and the more recent nested-hierarchy model, are able to describe food web structure satisfactorily [22]. The study of food webs holds great promise and may provide insights important for tackling a number of relevant ecological problems, including understanding potentially detrimental anthropogenic impacts on the diversity of life [20].

1.1.2 Metaecosystem

Communities of species that are connected by dispersal is called metaecosystem [23]. The exact definition of metaecosystem is up to debate [5]. The metaecosystem concept has the potential to integrate the perspectives of community ecology (i) to increase our ability to predict the consequences of land-use changes and habitat fragmentation on biodiversity and the provision of ecosystem services to human societies and (ii) to provide novel fundamental insights into the dynamics and functioning of ecosystems from local to global scales [24].

A number of researchers are now championing the importance of movement among local communities, under the rubric of metaecosystems, to understand both local and regional structure ([25], p. 224). Dispersal fre-

quently induces synchrony between spatially separated populations, in particular for random dispersal. The effect of dispersal depend on the exact nature and its intensity [5]. The questions of interest in metaecosystems are in numerous ways the same as for local ecosystems although the topology and dispersal behaviour can now affect the system properties differently[5].

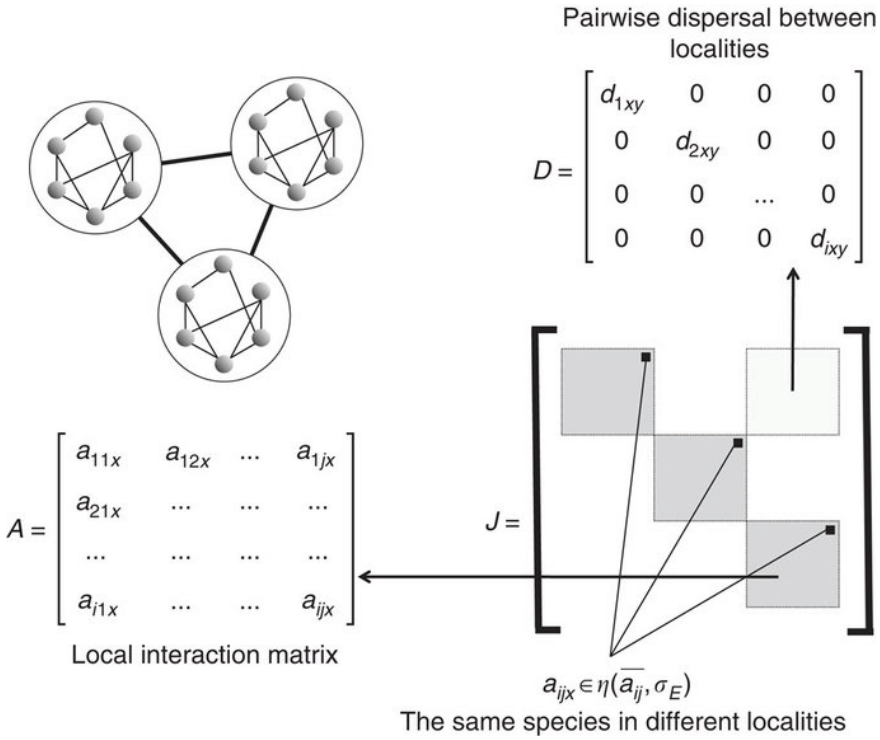

Figure 1.1: Illustration of the Jacobian matrix in random metaecosystems: The model represents the dynamics of a metaecosystem, pictured as a spatial network of interaction networks (top left). It is made of the sub-matrices A, M and D. The spatial heterogeneity among locations is implemented by varying interaction coefficients in space and the landscape is implemented by varying the spatial structure of the model. Figure taken directly from Gravel et al. [1].

1.2 Motivation

In ecology, a central issue is to uncover the basic determinants of the distribution of trophic interactions (ie, the structure of feeding relationships) among the members of natural communities [17]. To understand the factors and conditions that guarantee ecological systems persist is important [12]. Recent work has focused on other definitions of ecosystem stability

to explain the complexity-stability paradox [1]. Many hypotheses trying to explain this inconsistency have been invoked. Most of them have empirical support, but their relative or absolute importance is not well understood [1]. Some studies have focused on small food web modules which are conducted with different measurements of stability that are not comparable to May's local stability [1]. Others focused on the reason why distinct food web structures seem to be stable [5].

On the other hand, recent developments highlighted that the relationship between the structure of ecological networks and community stability depended on whether interactions were antagonistic (ie, predator-prey or bipartite) or mutualistic [27]. Both antagonistic and mutualistic were pointed out as structures that promote ecological stability [27]. Therefore, it is important to investigate models that include this kind of interactions between species [28]. On this matter, most literature has focused on single ecosystems or communities, therefore have focused on ecosystem or community matrix with the linearisation of the Lotka-Volterra equation at an equilibrium point. However, one of the important possibilities is that metaecosystems or metacommunities could be more stable [1]. In this thesis, the metacommunity perspective is considered, rather than metaecosystem.

1.3 Aim and objectives

The main aim of this thesis is to study the effect of dispersal on antagonistic interactions at a metacommunity scale. The question of whether large antagonistic metacommunities can be stable is addressed.

The dynamical properties of antagonistic interactions within a metacommunity are investigated. A Jacobian matrix is used to investigate the rate at which metacommunity of distinct localities returns to equilibrium following a disturbance.

1.4 Overview of the thesis

An introduction to the problem with background is presented in chapter 1. A review for the relevant literature that helped to determine the nature

of my research is discussed in chapter 2. The method used and results are described and presented in chapter 3 and 4. Chapter 5 present a conclusion and outlines the recommendation for future research.

Chapter 2

Literature review

In this chapter, literature related to the research question is reviewed. This helps to understand terminologies, the current state of the field, theory and methodologies for investigating the stability of ecological communities.

2.1 Ecological modelling

As defined in chapter 1 (section 1.1), ecological stability refers to the ability of a natural system to apply self-regulating mechanisms to return to equilibrium after a disturbance [3]. Ecological modelling is an important tool for investigating these types of dynamic behaviour patterns in populations, trophic interactions, and behavioural ecology [29]. A first step to mdel systems is to understand partially complex systems, mainly because an important characteristic of models is their flexibility, which allows a gradual introduction of complexity [29]. The ecological patterns that reflect population oscillations are often not clearly visible without analytical instruments such as ecological models [29]. Ecological theory is certainly an important ingredient of research programs concerned with monitoring and species control [29]. Understanding species fluctuation and predicting outbreaks are essential ingredients to support appropriate management decisions [29].

Ecologists have a fundamental academic interest that is tempered by resolving ecological complexity. That academic interest is important practical reality that ecology is increasingly being called upon to offer a leading role in identifying and solving pressing environmental problems [30]. Ecology is a

single discipline that integrates principles from various subfields, including evolutionary, population, community and ecosystem ecology [30].

2.2 Community ecology

The question of "why do species live here but not over there, but why do those species live over there and not here" is what drove McPeek's work ([25], p. 1). He defined species into four functional groups:

1. Coexisting species
2. Neutral species
3. Sink species
4. Walking dead species

but the idea of a set of coexisting species is the important organising concept throughout his book ([25], p. 9). The general statement of the ecological conditions required for invasibility, the fundamental criterion for coexistence, is that species will coexist with one another when no species in the set can deplete resource abundance/mutualist benefit or inflate enemy abundances to levels at which the other species cannot invade and support populations ([25], p. 72).

Note that invasibility and stability are not synonymous. Invasibility merely asks whether a species could invade or reinvade the community whereas stability questions whether any equilibrium point for the community is stable or unstable equilibrium. So even if any particular equilibrium is unstable, species may still not go extinct if the system displays limit cycles or chaotic dynamics ([25], p. 36). Coexisting species are species that can satisfy the invasibility criterion ([25], p. 10). The invasibility criterion determines whether a species has long-term advantage in a community that permits it to persist ([25], p. 24). Therefore, testing for coexistence fundamentally involves testing whether a species can increase when rare, ie, invasibility ([25], p. 11).

2.2.1 Traits

Traits are important in shaping the dynamics of species interactions and are what make species capable of satisfying the invasibility criteria in a particular local community, and so define which local communities a species can and cannot potentially occupy ([25], p. 267 - 268). The linkage between ecological and evolutionary dynamics is specified by how the traits of an individual interact with its environment to determine its overall fitness ([25], p. 85). Some traits such as body size may be almost universally important, however, even body size is not so important in every facet of demography and life history for every species ([25], p. 85).

The body mass of species has revealed itself to be a key property in modelling realistic food web structures and species interactions. Predator body mass is consistently one to two orders of magnitude larger than that of prey species and the metabolism of all species tends to scale allometrically [5]. In food webs, body size is the main trait mediating the interactions and might also mediate dispersal (both active and passive). Thus, a single trait for each species could determine all model parameters through appropriate functions [1]. However, body size is not a good trait for host-parasite system. The trait in host-parasite system is normally the chemical/immune response. Therefore, in consideration of traits (which are not considered in this thesis), one can look at the question: what kind of species trait will thrive or be suppressed in the system?

2.3 Theory of random matrices

Random Matrix Theory (RMT) is an active research area of modern mathematics and its main goal is to provide understanding of the diverse properties of matrices with entries drawn randomly from various probability distributions. The study of community matrices has a long history in ecology but so far methods relying on large random matrices have not been able to account for realistic food web structure, and were based on the simplifying assumption of a completely random network, in which every species has the same probability of interacting with each other [31].

Robert May [32] investigated the stability properties of large systems and found that they are less stable. The stability at one particular trophic level (eg, stability among competing predators) may promote general instability (eg, the escapes control of a herbivore species) [32]. Conversely, one particular trophic level may be unstable due to competition, then the effects of other levels (eg, predator) can lead to a total stable system [32]. To the contrary, stability at one trophic level, by feedback, should encourage stability at the other levels and the total web [32]. This view and the corollary that instability at any one level should tend to create an unstable total system is support by the intuition of the physical scientist [32].

Forty years ago, May [32] predicted that complexity and diversity should destabilise ecosystems [1, 12, 14, 33]. According to May, the theory that indicates stability for a random community must respect the following inequality

$$\sigma\sqrt{C(S-1)} < m,$$

where σ is the standard deviation of interspecific (ie, individuals of different species) interaction strength, C is the connectance (ie, the potential proportion interactions of species that are realised), S is the number of species and m is the average intraspecific (ie, individuals of same species) interaction strength [1].

2.4 Population abundance

Population abundances are always neglected in random matrix approaches and their role in determining stability is still not understood [13]. Considering feasibility constraints, ie, species in each community that can attain a positive equilibrium density, is important. Previous studies indicate that stability can be increased when applied to communities that are having positive values for all the species equilibrium densities [1]. For instance, the likelihood of having a feasible and unstable solution in the Lotka-Volterra system of equations decreases exponentially with the number of species for stable interaction matrices [13]. In ecological systems, the equilibrium point is meaningful only if the equilibrium abundances are all positive (ie, if the equilibrium is feasible) [12]. In feasible systems, stability increases with the

number of species and feasibility is a prerequisite to stability analysis [12].

Gibbs et al. [13] tackled a question of the effect of density dependence on the stability by explicitly including population abundances in a random matrix framework. They obtained an analytical formula that describes the spectrum of a large community matrix for arbitrarily feasible species abundance distributions and showed that density dependence do not affect stability qualitatively. Part of their goals was to extend the random matrix approach with a random density vector and determines the stability under two conditions: (i) addressing the effect of species abundance on stability and (ii) the relationship between feasibility (ie, all species have positive abundances) and stability.

Stone [33] developed methods to predict eigenvalue distribution of large complex Density Dependent (DD) systems and found that almost all feasible model systems are stable. The feasible equilibrium is stable if

$$\gamma = \sigma\sqrt{SC} < 1,$$

which surprisingly is independent of the positive equilibrium populations [33]. The community matrix is stable if the interaction matrix is stable. However, the abundance of species does not affect the sign of the eigenvalues [13]. Finding conditions leading to stable equilibria, ie, equilibria robust to small disturbance, is a key feature in understanding how persistent ecological systems are [33]. Dougoud et al. [12] also provided analytical results complemented by numerical simulations which show that it is almost impossible to find equilibria containing only positive abundances in species rich systems or, if so, the parameters are constrained to lead to ecologically nonsensical abundances in unstructured systems. Soon after the work of May, Roberts noted that May's approach indeed remained silent concerning the feasibility of the equilibrium [12].

2.5 Cascade effect

Indirect interactions that can control the entire ecosystem, occurring when a trophic level in a food web is suppressed are known as ecological cascade

effects (not considered in the thesis). It has been proposed that successful parasitoid species control is prevented because parasitiods are themselves hosts to other parasitoid (ie, hyperparasitoids) regulating their density [34]. Parasitoids supply an ecosystem service by controlling herbivorous insects and hyperparasitoids may supply an "ecosystem disservice" by disrupting parasitoid systems [34]. The current challenge is to understand the properties under which hyperparasitoids contribute to generate landscape-scale outbreaks in host-parasitoid systems [34]. Most studies refer to parasitoids while few have tracked hyperparasitiods under natural conditions, especially their role at the beginning of an outbreaks [34]. The impacts of hyperparasitism on the ecology and evolution of microbial pathogens in nature and its cascading effects throughout foodwebs is chronically underreseached [35].

Nenzén et al. [34] studied insect outbreaks caused by hyperparasitoids. They showed that the parasitoids are present everywhere at low density, therefore dispersal from other stands is not required [34]. For example, once a stand has a high density herbivore population, then dispersal is important such that they can disperse to seek for food and avoid mortality [34]. Long distance herbivore dispersal occurs with some probability, most occurs between neighbouring stands within 10-80 km [34]. Ultimately, hyperparasitoids cause mortality for both parasitoids and herbivores [34].

Donor control implies that food web dynamics are mainly controlled by resource availability (bottom-up control) [36]. This differs from many current food web hypotheses that theorise that predation controls food webs from top down [36]. Since Lindeman's (1942) study of food web dynamics, the debate over whether food webs are controlled top down or bottom up has continued [36]. Tritrophic food chain models that use a type II functional response produce trophic cascade when inputs to the bottom trophospecies are minimal [36].

For defoliating insects, parasitiods are known to be the most effective natural enemies that kill more individuals than both predators and parasites combined [34]. Dilation may cause the loss of parasitoids. This follows an increase in herbivore populations (ie, bottom-up), or may be the results of

a decrease in the parasitiod density (ie, top-down) [34]. Herbivore population density can be controlled effectively by parasitoids due to their unique trophic and reproduction life history [34]. Parasitoids lay eggs into an insect's body. Each parasitoid can lay up to 200 eggs into different insects and when that egg hatch, the larva feeds inside the insect and eventually cause insect death. The biological pest management relies on effective parasitoid control, yet traditional models still cannot explain the success and failure of parasitoid control [34].

Conclusion

In this thesis, ecological modelling is used to investigate the stability of ecological communities with antagonistic interactions. The stability criteria of predator-prey metacommunity are derived and simulations for complicated structures of bipartite interactions are obtained. The random matrix theory is followed to understand the properties of matrices with entries drawn from various probability distributions. Factors such as dispersal and populations abundance of species are considered. Other factors such as traits and cascade effects are not considered in this thesis. However, they are recommended for future studies in communities with antagonistic interactions.

Chapter 3

Antagonistic interactions

The structure of this chapter is as follows: In section 3.1, a bipartite model is formulated and stability is analysed for the four cases of its submodels. This is followed by the effect of density dependence on the community matrix of both predator-prey and bipartite interactions in section 3.1.3. The core part of this thesis is in section 3.2 and 3.3 where the effect of dispersal and density dependence on antagonistic metacommunities are investigated.

3.1 Bipartite community

Modelling is viewed as an important step towards better understanding and improved decision making. The most important ability of a modeller is to correctly decide on a suitable level of complexity to be applied in a system which is used as an attempt to understand interactions such as antagonistic systems [29]. Recently, the modelling approach has successfully spread to other disciplines, ranging from systems biology, neurosciences, through to atomic physics, finance, wireless and banking, making this a vibrant and exciting contemporary research discipline [33]. Both mathematical modelling and simulations are important in recent studies of biological mathematics [37].

3.1.1 Bipartite model

Ever since the work of Lotka and Volterra, ecologists attempted to mathematise the interactions between species to build predictive models of population dynamics [13]. Mathematical network models can be used to simplify

the vast complexity of the real world, to formally describe and investigate ecological phenomena, and to understand how ecosystems react to stress and disturbances [38]. Below is a general bipartite model which represents the dynamics of host given its interaction with parasite. The model is formulated using ordinary differential equations (ODEs) following Gravel et al. [1] model which was derived from the Lotka-Volterra model. The general system of the Lotka-Volterra population dynamics model is given by

$$\begin{aligned} \frac{dH_i}{dt} &= H_i \left(r_i - \sum_{j=1}^{S_p} b_{ij} P_j \right) \\ \frac{dP_j}{dt} &= P_j \left(-q_j + \sum_{i=1}^{S_h} e_{ij} b_{ij} H_i \right), \end{aligned} \tag{3.1}$$

where the variables and parameters are defined in Table 3.1.

Table 3.1: State variables and parameters description for a bipartite model.

State variable	Description
H_i	Population abundance of host i.
i	Subscript indexing host species.
S_h	Total number of host species.
P_j	Population abundance of parasite j.
j	Subscript indexing parasite species.
S_p	Total number of parasite species.
Parameter	**Description**
r_i	Intrinsic population grow rate of host i.
b_{ij}	Attack coefficient of parasite j feeding on host i.
e_{ij}	Conversion efficiency for parasite j feeding on host i.
q_j	Death rate of parasite j.

3.1.2 Stability analysis

Here, we start by constructing four different submodels from the above general host-parasite model 3.1 and study their stability behaviour respectively. In each submodel, both linear (ie, Malthusian) and logistic growth rates are considered for the host populations. Note that this models have been explored widely in the literature. Therefore, this serves as an approach and

introduction to the community matrix with many species (see section 3.1.3). The submodels are as follows

1. One host-one parasite
2. One host-two parasite
3. Two host-one parasite
4. Two host-two parasite.

For a system to be stable, this can be illustrated by calling a particular eigenvalue λ that is written as $\lambda = x + iy$, then

i) If $x > 0$, the system is unstable

ii) If $x < 0$, the system is stable

iii) If $x = 0$, the asymptotically dominant component is purely oscillatory, neither growth nor being damped.

3.1.2.1 One host-one parasite

A simple one host-one parasite system is given by

$$\begin{aligned} \frac{dH}{dt} &= H(r - bP) \\ \frac{dP}{dt} &= P(-q + ebH) \end{aligned} \tag{3.2}$$

and its equilibria are $E_0 = (0, 0)$ and $E_1 = (\frac{q}{eb}, \frac{r}{b})$. Note that

- E_0 is a point where both species are absent, meaning there is no host or parasite at that point. This point is ecologically meaningless.
- E_1 is a point where both species coexist, ie, both host and parasite are present. Therefore, analysis can be conducted.

The point where nullclines intersect the axes of the other species (ie, equilibrium points) are critical for understanding invasibility because these points define the abundances of the other species birth and death rates when focal species rare ([25], p. 35) (see figure 3.1). The Jacobian matrix of a one host-one parasite system is given by

$$J(H,P) = \begin{bmatrix} \frac{\partial \dot{H}}{\partial H} & \frac{\partial \dot{H}}{\partial P} \\ \\ \frac{\partial \dot{P}}{\partial H} & \frac{\partial \dot{P}}{\partial P} \end{bmatrix} = \begin{bmatrix} r - bP & -bH \\ \\ ebP & ebH - q \end{bmatrix}$$

now, substituting the point where two steady states intersect, ie, E_1 into the Jacobian matrix, gives

$$J_{E_1}(H^*, P^*) = \begin{bmatrix} 0 & -\frac{q}{e} \\ \\ er & 0 \end{bmatrix}$$

and computing the eigenvalues of J_{E_1}, ie, $\det|J_{E_1} - \lambda I| = 0$, we get the following characteristic equation

$$\begin{aligned} \lambda^2 + rq &= 0 \\ \lambda &= \pm i\sqrt{rq}\,. \end{aligned}$$

Purely imaginary eigenvalues cases in nonlinear systems are open to more than one interpretation. In the above case, there are no real parts of the solution (see Figure 3.2). Therefore purely imaginary roots imply that the linearised system is on the cutting edge between instability and asymptotic stability and on the edge between oscillatory solutions that increase in amplitude and those that decrease in amplitude ([39], p. 113).

Equation 3.2 can also be written in a dimensionless form in order to reduce number of parameters. let $H = c_1 x$, $P = c_2 y$ and $t = c_3 \tau$. Substitute H, P, and t into 3.2 to obtain

$$\begin{aligned} \frac{c_1 dx}{c_3 dt} &= r(c_1 x) - b(c_1 x)(c_2 y) = rc_1(x) - bc_1 c_2(xy) \\ \frac{c_2 dy}{c_3 dt} &= eb(c_1 x)(c_2 y) - d(c_2 y) = ebc_1 c_2(xy) - qc_2(y) \end{aligned}$$

$$\begin{aligned} \Rightarrow \frac{dx}{dt} &= rc_3(x) - bc_2 c_3(xy) \\ \Rightarrow \frac{dy}{dt} &= ebc_1 c_3(xy) - qc_3(y). \end{aligned}$$

If $c_3 = \frac{1}{r}$, then let $bc_2c_3 = 1$ and $ebc_1c_3 = 1$, so that $c_2 = \frac{r}{b}$, and $c_1 = \frac{r}{eb}$ which gives

$$\frac{dx}{dt} = x - xy$$
$$\frac{dy}{dt} = xy - \frac{q}{r}y.$$

Finally substitute c_1, c_2, and c_3 into dimensionless variable where $x = \frac{ebH}{r}$, $y = \frac{bP}{r}$, $\tau = rt$, and also let control parameter $\mu = \frac{q}{r}$. Figure 3.1 below is the phase portrait of the one host-one parasite system.

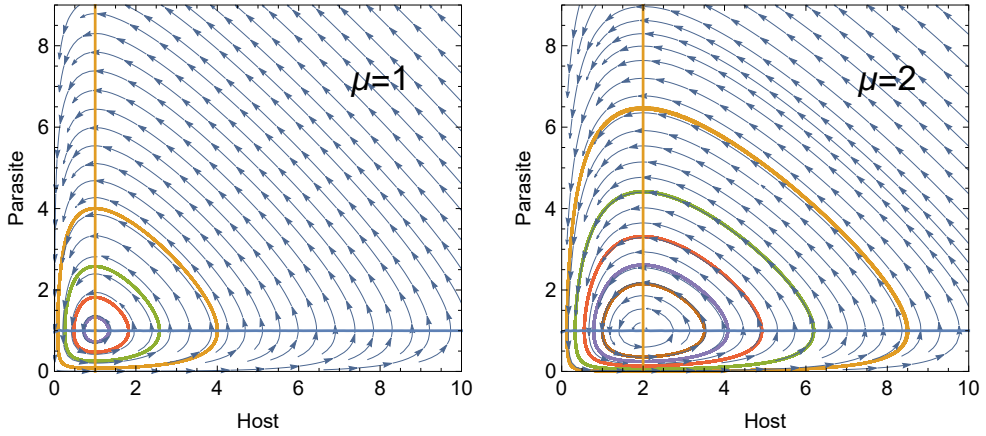

Figure 3.1: Phase portrait for a host-parasite showing a center (ie, neutral closed orbits around the equilibrium). The vector field shows equilibria at $(1,1)$ and $(2,1)$ when $\mu = 1$ and $\mu = 2$ respectively. Nullclines are the x-axis, y-axis, the lines $(x,y) = (1,1)$ in the left panel and $(x,y) = (2,1)$ in the right panel. The curves shown are the solutions travelling periodically in the counterclockwise direction.

Coexistence also implies that the nullclines intersect one another at positive abundance for both species, giving $H^* > 0$ and $P^* > 0$, but it does not imply that this equilibrium point is stable ([25], p. 35).

According to McPeek [25], the host can invade the system if $\frac{r}{b} > 0$ and the parasite can invade the system if the host is present and if $\frac{q}{eb} > 0$. So, in order words, because these two species can invade when rare and the other species is at its demographic equilibrium in its absence, these two species coexist.

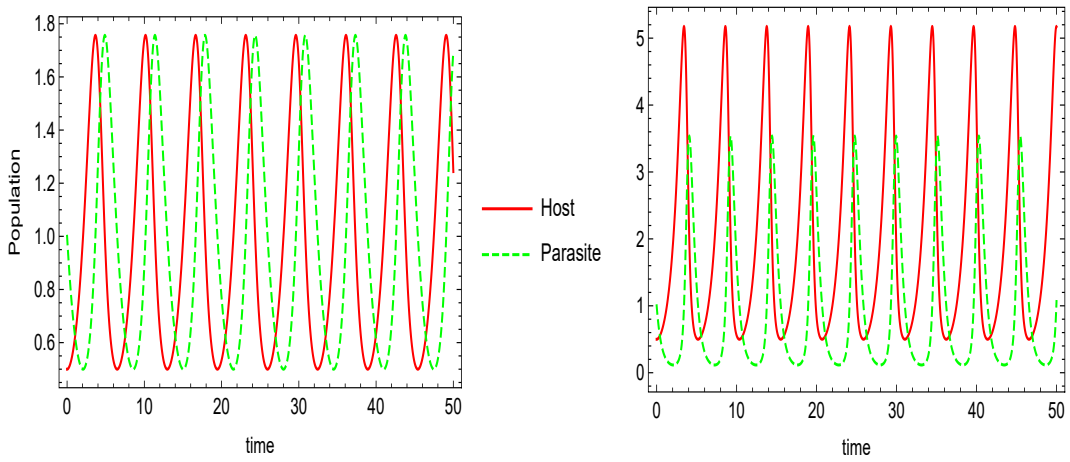

Figure 3.2: Simulation system of a one host-one parasite. The initial conditions are $x(0) = 0.5$, $y(0) = 1.0$, the coefficient has the proportion $\mu = 1$ on the left panel and $\mu = 2$ on the right panel.

Now, submodel 3.2 is adjusted to include logistic growth rate in the host species as given below

$$\begin{aligned} \frac{dH}{dt} &= rH\left(1 - \frac{H}{K}\right) - bPH \\ \frac{dP}{dt} &= P\left(-q + ebH\right), \end{aligned}$$

then the real part of the eigenvalue that gives the stability criterion is given by

$$Re(\lambda) = \frac{1}{2}\left(r + ebH^* - bP^* - q - \frac{2rH^*}{K}\right). \tag{3.3}$$

This system is stable if $Re(\lambda) < 0$ (see Figure 3.3). In the one host-one parasite case, the system with linear growth, behaves as a centre. The trajectories around the critical point produce constant, circular closed orbits and the system is neutrally stable. The system with logistic growth rate is stable (see Table 3.2).

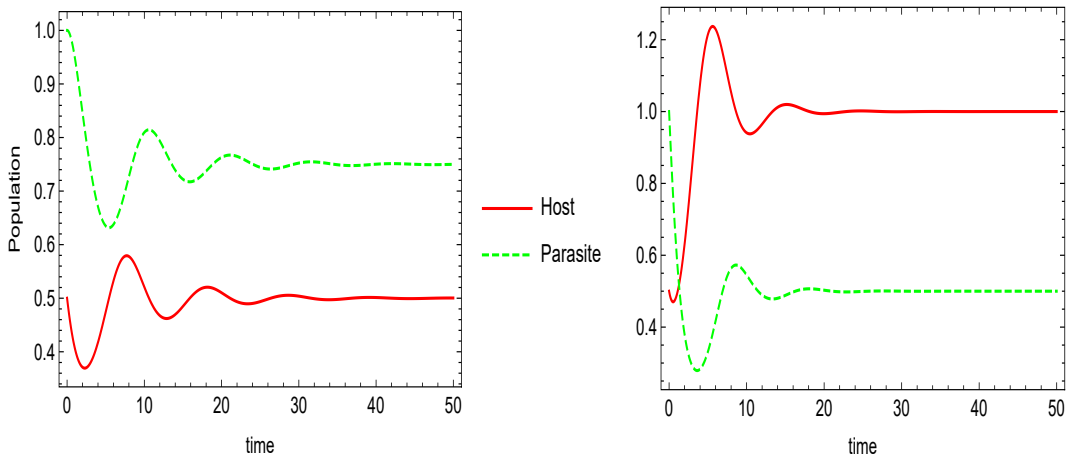

Figure 3.3: Simulation system of logistic growth rate of a one host-one parasite. The initial conditions are $x(0) = 0.5$, $y(0) = 1.0$, $K = 2$, the coefficient has the proportion $\mu = 0.5$ on the left panel and $\mu = 1$ on the right panel.

3.1.2.2 One host-two parasite

For a one host-two parasite case, the following submodel is constructed from model (3.1)

$$\begin{aligned} \frac{dH}{dt} &= H\left(r - b_1P_1 - b_2P_2\right) \\ \frac{dP_1}{dt} &= P_1\left(eb_1H - q_1\right) \\ \frac{dP_2}{dt} &= P_2\left(eb_2H - q_2\right). \end{aligned} \tag{3.4}$$

The three equilibria obtained are $E_0 = (\frac{q_2}{eb_2}, 0, \frac{r}{b_2})$, $E_1 = (\frac{q_1}{eb_1}, \frac{r}{b_1}, 0)$ and $E_2 = (0, 0, 0)$. Note that E_2 is ecologically meaningless. Therefore, substituting E_0 and E_1 into the Jacobian matrix and determine its eigenvalues respectively gives

$$\begin{aligned} J_{E_0} &:= \left(-\frac{b_2q_1 + b_1q_2}{b_2}, -i\sqrt{rq_1}, i\sqrt{rq_1}\right) \\ J_{E_1} &:= \left(\frac{b_2q_1 + b_1q_2}{b_1}, -i\sqrt{rq_1}, i\sqrt{rq_1}\right). \end{aligned}$$

The eigenvalues show that this system is unstable. A system with logistic growth rate of host is given in a nondimensional form as

$$\begin{aligned}\frac{dx}{dt} &= x\left(1-\frac{x}{k}\right)-x(y+z)\\ \frac{dy}{dt} &= y\left(x-\mu_1\right)\\ \frac{dz}{dt} &= z\left(x-\mu_2\right).\end{aligned}$$

Its eigenvalues are complicated to be computed analytically. However, simulation shows that the two parasite cannot coexist an a single host (see Figure 3.4).

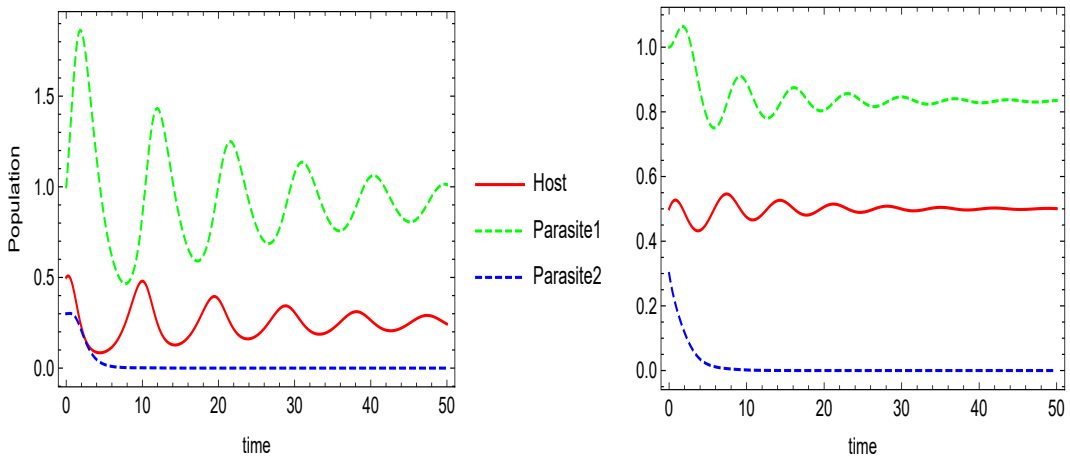

Figure 3.4: Simulation system of a one host-two parasite. The initial conditions are $x(0) = 0.5$, $y(0) = 1.0$, $z(0) = 0.3$, the coefficients have the proportions $K = 3$, $(\mu_1, \mu_2) = (0.5, 1)$ on the left panel and $(\mu_1, \mu_2) = (1, 1.5)$ on the right panel.

3.1.2.3 Two host-one parasite

For a two host-one parasite case, the following submodel is derived from model 3.1

$$\begin{aligned}\frac{dH_1}{dt} &= H_1\left(r_1-b_1P\right) \qquad (3.5)\\ \frac{dH_1}{dt} &= H_2\left(r_2-b_2P\right)\\ \frac{dP}{dt} &= P\left(eb_1H_1+eb_2H_2-q\right).\end{aligned}$$

Letting $x = \frac{eb_1H_1}{r_1}$, $y = \frac{eb_2H_2}{r_1}$, $z = \frac{b_1P}{r_1}$, $\tau = r_1t$ and $\mu = \frac{q}{r_1}$, the system's nondimensional form is given by

$$\begin{aligned}\frac{d(x+y)}{dt} &= (x+y)(1-z)\\ \frac{dz}{dt} &= z(x+y-\mu).\end{aligned}$$

This nondimensional equation of a two host-one parasite system does not give solutions for all variables. This indicates that the coexistence of such systems does not exist. When logistic growth of the host is added to sub-model 3.5 as follows

$$\begin{aligned}\frac{dH_1}{dt} &= r_1H_1\left(1-\frac{H_1}{K_1}\right)-b_1H_1P\\ \frac{dH_2}{dt} &= r_2H_2\left(1-\frac{H_2}{K_2}\right)-b_2H_2P\\ \frac{dP}{dt} &= P(eb_1H_1+eb_2H_2-q),\end{aligned} \tag{3.6}$$

and its nondimensional form is given by

$$\begin{aligned}\frac{dx}{dt} &= x\left(1-\frac{x}{k_1}\right)-xz\\ \frac{dy}{dt} &= y\left(1-\frac{y}{k_2}\right)-yz\\ \frac{dz}{dt} &= z(x+y-\mu),\end{aligned}$$

where nondimensional parameter $\mu = \frac{q}{r}$. Assume that $r_1 = r_2$, the steady state of interest is $\{\frac{K_1\mu}{K_1+K_2}, \frac{K_2\mu}{K_1+K_2}, -\frac{\mu-K_1+K_2}{K_1+K_2}\}$ which exist if $1-\frac{\mu}{K_1+K_2} > 0$. The real part of the eigenvalues are negative and simulation shows that the system is stable (see Figure 3.5).

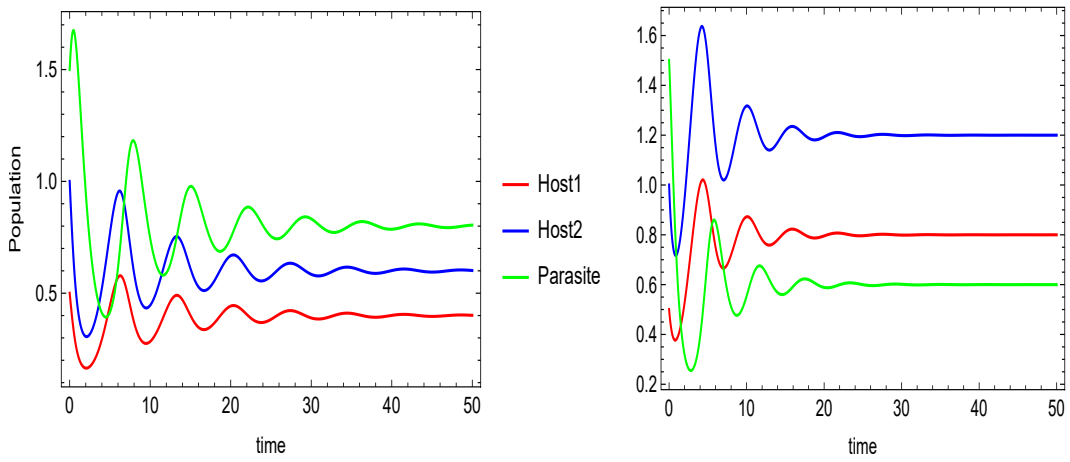

Figure 3.5: Simulation system of a two host-one parasite. The initial conditions are $x(0) = 1.0$, $y(0) = 1.0$, $z(0) = 1.0$, the coefficients have the proportions $k_1 = 2$, $k_2 = 3$, $\mu = 1$ on the left panel and $\mu = 2$ on the right panel.

Additionally, a system with competition between hosts in a two host-one parasite case can be explored. Model 3.6 can be adjusted to

$$\begin{aligned} \frac{dH_1}{dt} &= r_1 H_1 \left(1 - \frac{H_1 + a_1 H_2}{K_1}\right) - b_1 H_1 P \\ \frac{dH_2}{dt} &= r_2 H_2 \left(1 - \frac{a_2 H_1 + H_2}{K_2}\right) - b_2 H_2 P \\ \frac{dP}{dt} &= P\left(e b_1 H_1 + e b_2 H_2 - q\right), \end{aligned} \tag{3.7}$$

with a nondimensional form given by

$$\begin{aligned} \frac{dx}{dt} &= x\left(1 - \frac{x + a_1 y}{k_1}\right) - xz \\ \frac{dy}{dt} &= y\left(1 - \frac{a_2 x + y}{k_2}\right) - yz \\ \frac{dz}{dt} &= z\left(x + y - \mu\right). \end{aligned}$$

Simulation of a two host-one parasite system with competition between two hosts is shown in Figure 3.6.

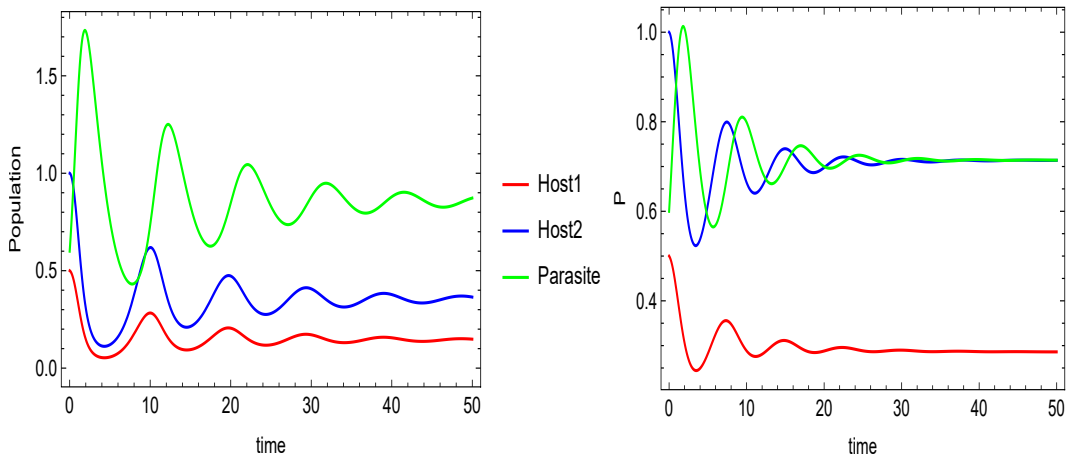

Figure 3.6: Simulation system of a two host-one parasite with competition of host. The initial conditions are $x(0) = 0.5$, $y(0) = 1.0$, $z(0) = 0.6$, the coefficients have the proportions $k_1 = 2$, $k_2 = 3$, $a_1 = 0.4$, $a_2 = 0.5$, $\mu = 0.5$ on the left panel and $\mu = 1$ on the right panel.

3.1.2.4 Two host-two parasite

For a two host-two parasite case, the submodel derived from model 3.1 is given by

$$\begin{aligned}
\frac{dH_1}{dt} &= H_1\left(r_1 - b_{11}P_1 - b_{12}P_2\right) \qquad (3.8)\\
\frac{dH_2}{dt} &= H_2\left(r_2 - b_{21}P_1 - b_{22}P_2\right)\\
\frac{dP_1}{dt} &= P_1\left(eb_{11}H_1 + eb_{12}H_2 - q_1\right)\\
\frac{dP_2}{dt} &= P_2\left(eb_{21}H_1 + eb_{22}H_2 - q_2\right).
\end{aligned}$$

From the submodel, four equilibria $(H_1^*, H_2^*, P_1^*, P_2^*)$,ie, $E_0 = (0,0,0,0)$, $E_1 = (0, \frac{q_2}{eb_{22}}, 0, \frac{r_2}{b_{22}})$, $E_2 = (\frac{q_1}{eb_{11}}, 0, \frac{r_1}{b_{11}}, 0)$ and $E_3 = \left(\frac{r_2 b_{12} q_1}{e r_1 (b_{12}b_{21} - b_{11}b_{22})}, \frac{q_2(r_1 b_{21} - r_2 b_{11})}{e r_2 (b_{12}b_{21} - b_{11}b_{22})}, \frac{r_2 b_{12} - r_1 b_{22}}{(b_{12}b_{21} - b_{11}b_{22})}, \frac{r_1 b_{21} - r_2 b_{11}}{(b_{12}b_{21} - b_{11}b_{22})}\right)$ are obtained. Substituting E_3 into the Jacobian matrix as a steady state of interest, using Mathematica, it shows the positive real parts for all the eigenvalues. Therefore this system is unstable.

However, when logistic growth rate of the two hosts is considered, its nondimensional form is as follows

$$\begin{aligned}
\frac{dx}{dt} &= x\left(1-\frac{x+a_1y}{k_1}\right)-x(z+w)\\
\frac{dy}{dt} &= y\left(1-\frac{a_2x+y}{k_1}\right)-y(z+w)\\
\frac{dz}{dt} &= z(x+y-\mu_1)\\
\frac{dw}{dt} &= w(x+y-\mu_2).
\end{aligned}$$

Simulation of a two host-two parasite system is illustrated in Figure 3.7 (see stability analysis in Table 3.2).

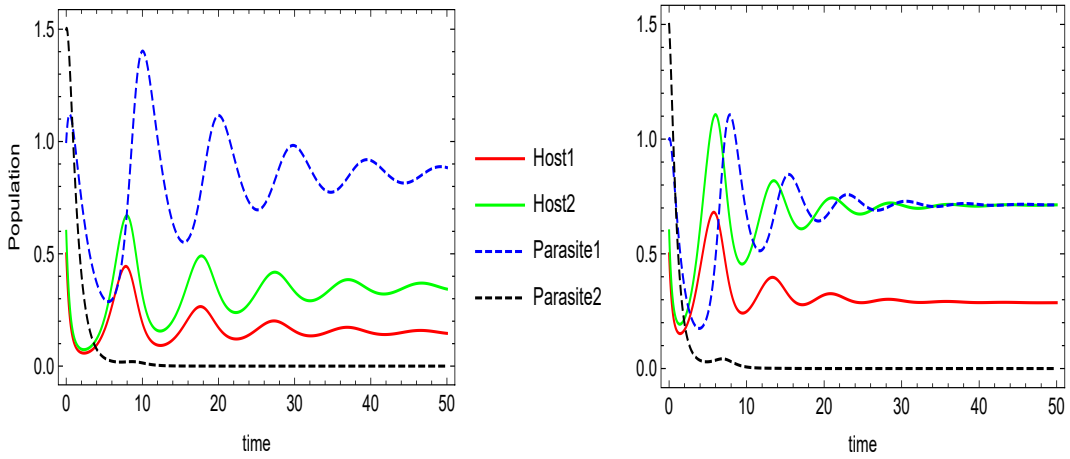

Figure 3.7: Simulation system of a two host-two parasite. The initial conditions are $x(0) = 0.5$, $y(0) = 0.6$, $z(0) = 1.0$, $w(0) = 1.5$, the coefficients have the proportions $k_1 = 2$, $k_2 = 3$, $a_1 = 0.4$, $a_2 = 0.5$, $(\mu_1, \mu_2) = (0.5, 1)$ on the left panel and $(\mu_1, \mu_2) = (1, 1.5)$ on the right panel.

Table 3.2: Stability analysis of the four submodels from the general host-parasite model 3.1.

Submodel	Stability analysis
One host-one parasite	For linear growth, the system behaves as a centre and is neutrally stable. For logistic growth, the system is stable.
One host-two parasite	For linear growth, the system is unstable. For logistic growth, simulation shows that the two parasite does not coexist as one goes extinct.
Two host-one parasite	For linear growth, the coexistence of this system does not exist. For logistic growth, the system is stable.
Two host-two parasite	For linear growth, the system is unstable. For logistic growth, three species coexist and a parasite goes extinct.

3.1.3 Community matrix

In this section, many species in a single community are considered (ie, local community). Robert May showed that a many predator-many prey system is less stable than a one predator-one prey community [32]. The stability of large ecological systems has been investigated for more than forty years [11, 31] as mentioned in chapter 2. This is done by first showing how Allesina and Tang [14] constructed a predator-prey food web matrix following the predator-prey matrix algorithm from their supplementary information. The community matrix determines the effects of one species on another around a feasible equilibrium point: if all the eigenvalues of matrix have a negative real part, the equilibrium is locally stable [31]. However, according to Allesina and Tang, the stability criterion of a predator-prey community should follow the inequality:

$$\sqrt{SC} < \frac{\theta\pi}{\pi - 2}, \tag{3.9}$$

where S is the number of species, C is the connectance, $\theta = \frac{m}{\sigma}$ where m and σ are intraspecific interaction strength and interspecific interaction strength

respectively. Allesina and Tang found that predator-prey is the type of network that is more likely to be stable than expected at random [31].

The Jacobian matrix is obtained by linearising the system of equations describing the dynamics of all species in a community at equilibrium [1]. Therefore, the Jacobian matrix J of a local community is given by the sum of two matrices

$$J = M + A, \tag{3.10}$$

where M is a diagonal matrix that represent intraspecific density dependence, with values $-m_i$ along the diagonal and 0s in the rest of the matrix. A is the local Jacobian matrix, describing interspecific interactions following Allesina and Tang predator-prey matrix algorithm. Figure 3.8 below, illustrates the eigenvalues distribution in the complex plane for local community of predator-prey matrix.

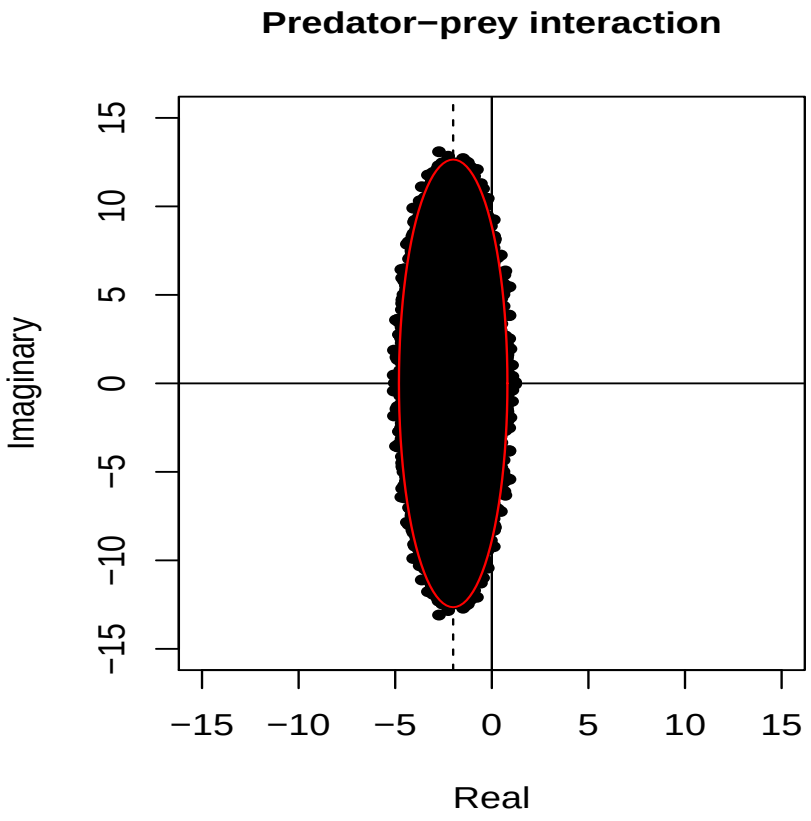

Figure 3.8: Illustration of the eigenvalues distribution in the complex plane. $S = 250$, $n = 20$ $C = 0.3$, $\sigma = 1$ and $m = 2$ on the diagonal and off-diagonal elements following predator-prey prescriptions. The eigenvalues of large predator-prey matrices are contained in a red vertically stretched ellipse, centred at $(-m, 0)$, with horizontal radius $\sigma\sqrt{CS}(1 - 2/\pi)$.

3.1.3.1 Density dependence

The prediction of a community's response to disturbance is a challenging task in ecology [40]. Here, the effect of density dependence on the stability of predator-prey community matrix is explored. The Jacobian matrix is constructed as follows,

$$J = X(M + A) \tag{3.11}$$

where X is a vector decribed as diagonal matrix with $X_{ii} = x_i^*$ and zeros elsewhere. The log-series distribution, discrete lognormal and negative binomial have been proposed to describe the empirical species abundances

(SADs) that emerge from either niche or neutral mechanisms [13]. The feasible equilibrium x_i^* is stable if

$$\gamma = \sigma\sqrt{SC} < 1,$$

which surprisingly is independent of the positive equilibrium populations. In terms of model parameters, the threshold criterion ($\gamma = \sigma\sqrt{SC} < 1$) means that if either S, σ or C become too large, then the system will turn into an unstable regime [33]. Many previous studies of biological networks have been unable to determine the stability properties of the community matrix $X(M + A)$ for large complex random matrix systems. This is considered an unsolved and open problem [33]. Figure 3.9 and 3.10 illustrates the eigenvalues distribution of a density dependent community matrix with predator-prey interaction.

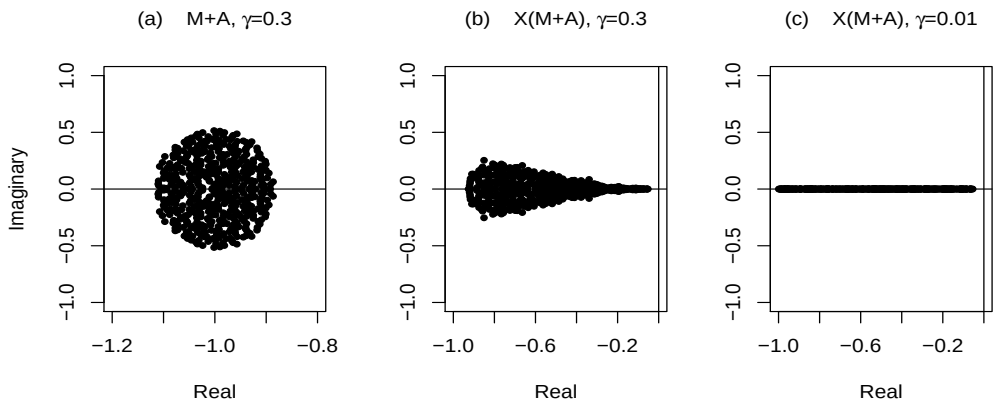

Figure 3.9: (**a**) Eigenvalues distribution of the matrix $M + A$ in the complex plane for $S = 500$, $\gamma = 0.3$ are distributed according to the circular law and fall in a centred at $(-1, 0)$ having radius γ. (**b**) The eigenvalues distribution for the community matrix $X(M + A)$, where $X = diag(x_i^*)$ is a positive diagonal matrix with the same matrix $M + A$ in (**a**). The circular distribution disappears and is replaced by a "guitar-shaped" distribution in which the imaginary components of the eigenvalues appear flattened out compared with (**a**). (**c**) Same as (**b**) but with $\gamma = 0.01$. The diagonal entries of matrix X are sampled from a uniform distribution on [0.05,1].

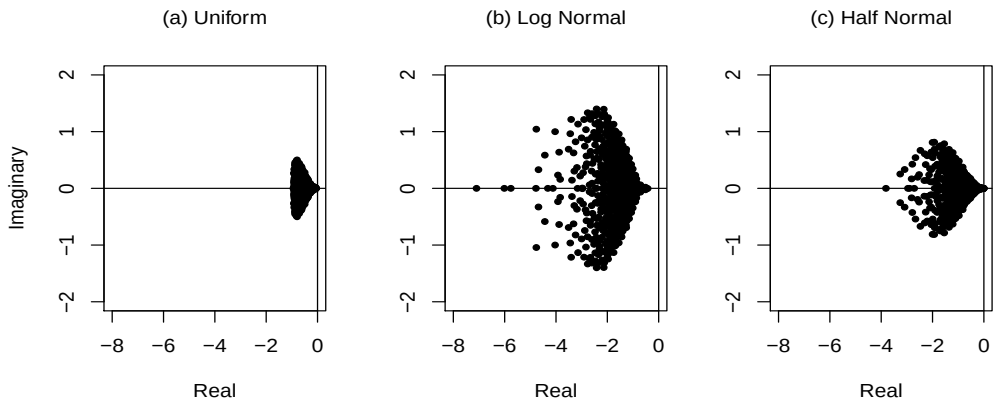

Figure 3.10: Eigenvalues distribution of the spectrum of $X(M + A)$. (**a**) X is sampled from a uniform distribution on $[0.25, 1.75]$, (**b**) X is sampled from a log-normal distribution with log-mean 0.5 and log-standard deviation 0.5, (**c**) X is sampled from a half-normal with parameter $\theta = 1$

The density dependence stabilises the predator-prey community matrix. According to simulation, the matrix entries sampled from log normal are more stable that entries sampled from half normal distribution.

3.1.4 Generating a community matrix with bipartite interaction model

In this section, a community matrix with two trophic levels of host-parasite interactions is explored. A matrix system of host H and parasite P populations, whose dynamics is described by equation 3.1 is considered below

$$\mathbf{A} = \begin{pmatrix} -\mathbf{C} & -\mathbf{B} \\ \\ \mathbf{E}\mathbf{B}^{\mathbf{T}} & \mathbf{0} \end{pmatrix}, \tag{3.12}$$

where $\mathbf{C}$ is an $S_h \times S_h$ nonnegative matrix of intraspecific competition, $\mathbf{B}$ is an $S_h \times S_p$ nonnegative matrix and $\mathbf{E}$ is an $S_p \times S_p$ nonnegative matrix. If $\mathbf{C}$ is a positive diagonal matrix, then any feasible equilibrium point is asymptotically stable (see Figure 3.10a). When $\mathbf{C}$ is not diagonal, then the feasible equilibrium point can be proven to be asymptotically stable. The matricial form of equation 3.1 is given by

$$\begin{aligned} \dot{H} &= H(r - BP) \\ \dot{P} &= P(-q + EB^T H) \end{aligned} \tag{3.13}$$

that is

$$\dot{N} = diag(N)(R + AN) \tag{3.14}$$

where

$$N = \begin{bmatrix} H_1 \\ \vdots \\ H_{S_h} \\ P_1 \\ \vdots \\ P_{S_p} \end{bmatrix}, R = \begin{bmatrix} r_1 \\ \vdots \\ r_{S_h} \\ -q_1 \\ \vdots \\ -q_{S_p} \end{bmatrix} \text{ and } A = \begin{bmatrix} -c_{11} & \cdots & -c_{1S_h} & -b_{11} & \cdots & -b_{1S_p} \\ \vdots & \cdots & \vdots & \vdots & \cdots & \vdots \\ -c_{S_h 1} & \cdots & -c_{S_h S_h} & -b_{S_h 1} & \cdots & -b_{S_h S_p} \\ eb^t_{11} & \cdots & eb^t_{S_h 1} & 0 & \cdots & 0 \\ \vdots & \cdots & \vdots & \vdots & \cdots & \vdots \\ eb^t_{1S_p} & \cdots & eb^t_{S_h S_p} & 0 & \cdots & 0 \end{bmatrix}$$

therefore

$$\dot{N} = \begin{bmatrix} H_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & \ddots & 0 & 0 & 0 & 0 \\ 0 & 0 & H_{S_h} & 0 & 0 & 0 \\ 0 & 0 & 0 & P_1 & 0 & 0 \\ 0 & 0 & 0 & 0 & \ddots & 0 \\ 0 & 0 & 0 & 0 & 0 & P_{S_p} \end{bmatrix} \left(\begin{bmatrix} r_1 \\ \vdots \\ r_{S_h} \\ -q_1 \\ \vdots \\ -q_{S_p} \end{bmatrix} + \begin{bmatrix} c_{11} & \cdots & c_{1S_h} & -b_{11} & \cdots & -b_{1S_p} \\ \vdots & \cdots & \vdots & \vdots & \cdots & \vdots \\ c_{S_h1} & \cdots & c_{S_hS_h} & -b_{S_h1} & \cdots & -b_{S_hS_p} \\ eb^t_{11} & \cdots & eb^t_{S_h1} & 0 & \cdots & 0 \\ \vdots & \cdots & \vdots & \vdots & \cdots & \vdots \\ eb^t_{1S_p} & \cdots & eb^t_{S_hS_p} & 0 & \cdots & 0 \end{bmatrix} \begin{bmatrix} H_1 \\ \vdots \\ H_{S_h} \\ P_1 \\ \vdots \\ P_{S_p} \end{bmatrix} \right)$$

From equation 3.14, a vector N^* is a fixed point (ie, equilibrium) if

$$0 = diag(N^*)(R + AN^*). \tag{3.15}$$

An equilibrium point is feasible if $N^* > 0$ for all its elements. A feasible equilibrium point (if it exists) is a solution to the equation given by

$$R = -AN^* \tag{3.16}$$

and therefore, assuming A is invertible, then

$$N^* = -(A^{-1})R. \tag{3.17}$$

An equilibrium point N^* is stable if the system returns to it following any small disturbance of the population abundances. Therefore, the Jacobian (ie, community matrix) that evaluates at the equilibrium point is

$$J = diag(N^*)A. \tag{3.18}$$

According to Grilli et al. [41], to ensure feasibility, vector R can be chosen accordingly. This allows to see if the system is feasible (ie, if all components of N^* are positive). Vector R collects the growth and death rates for the host and parasite respectively such that $r_i > 0$ for all $i = 1, ..., S_h$ and $q_j < 0$ for all $j = 1, ..., S_p$. If R does not lead to positive N^* then it is not in the feasibility domain.

An equilibrium point is stable if it is the final outcome of the dynamics from any initial condition that involves positive population abundance [41], (see Figure 3.10b). Grilli et al. [41] studied the proportion of conditions leading to stable and feasible equilibria (ie, the number of combinations of the growth or death rate R out of all possible combinations). For a stable matrix A, this means that R should satisfy feasibility of N^*.

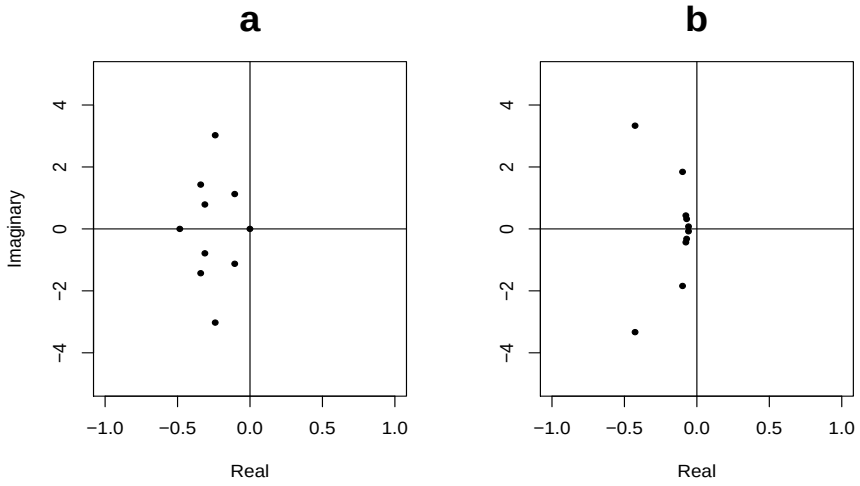

Figure 3.11: Illustration of the eigenvalues distribution in the complex plane. Distribution of the eigenvalues of matrix **A** in the complex plane when (**a**) $S = 5$, $\sigma = 1$, $c = 1$, $e = 0.5$ and **C** is a positive diagonal matrix and (**b**) when matrix $\mathbf{J} = diag(\mathbf{N}^*)\mathbf{A}$ where $\mathbf{N}^* = -(A^{-1})R$ and R contains growth rates $r_i > 0$ and death rates $q_j < 0$ distributed from half-normal distribution.

Now, the method used by Stone (discussed in chapter 2.4) to predict eigenvalue distribution of large complex density dependence (DD) systems, ie, community matrix $\mathbf{J} = \mathbf{N}^*\mathbf{A}$ where $\mathbf{N}^*$ is a diagonal matrix of population equilibrium values, is explored. If bipartite matrix **A** is locally stable, then the community matrix $\mathbf{J} = \mathbf{N}^*\mathbf{A}$ is also locally stable, provided the system is feasible (ie, all species have positive equilibria $\mathbf{N}^* > 0$) (see Figure 3.11 b).

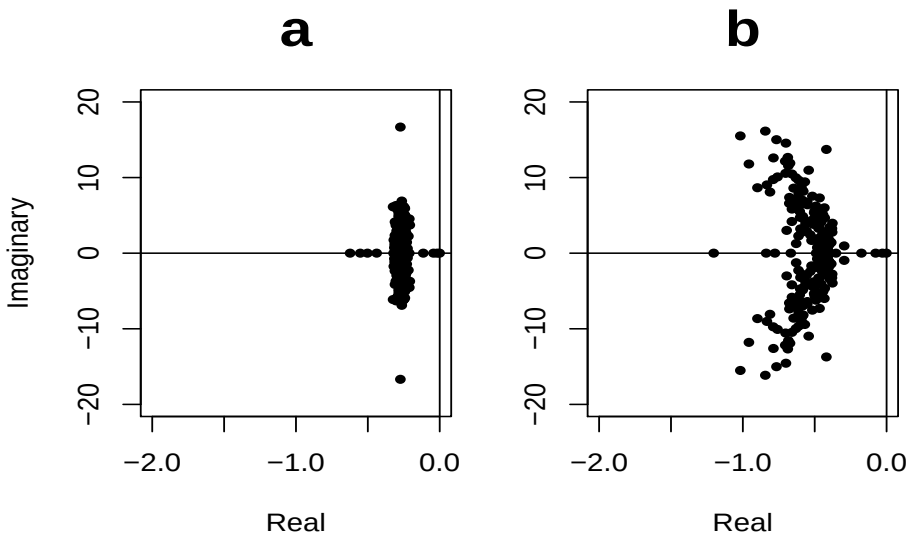

Figure 3.12: Illustration of the eigenvalues distribution in the complex plane. Distribution of eigenvalues of the matrix $\mathbf{A}$ in the complex plane when (**a**) $S = 100, \sigma = 1, c = 0.3, e = 0.5$ and $\mathbf{C}$ is a positive diagonal matrix and (**b**) when matrix $\mathbf{J} = \mathbf{N}^*\mathbf{A}$ where $\mathbf{N}^*$ is a positive diagonal matrix that is distributed from log-normal distribution.

Simulation for bipartite community matrix shows that it is almost impossible to have all positive density dependence generated on the real Jacobian for large bipartite interactions. Although the system is stable for 5 species as shown in Figure 3.11. Hence, Stone's method is useful for large communities (see Figure 3.12).

3.2 Bipartite metacommunity

Emigration and immigration generate population demographic rates comparable to death and birth rates respectively. These rates of movement generate various forms of density dependence that interact with local mechanisms of population regulation to shape local abundances and population dynamics ([25], p. 225). In this section, the effect of dispersal on metacommunity size and stability is explored for communities that disperse passively between multiple distinct habitat patches. Model 3.1 is reconstructed to represent the dynamics of species i at location x interacting with all S_p species j in x, and dispersal to and from all other n locations:

$$\begin{aligned}\frac{dH_{ix}}{dt} &= H_{ix}\left(r_{ix} - \sum_{j=1}^{S_p} b_{ijx}P_{jx}\right) + \Delta H_{ix} \\ \frac{dP_{jx}}{dt} &= P_{jx}\left(-q_{jx} + \sum_{i=1}^{S_h} e_{ijx}b_{ijx}H_{ix}\right) + \Delta P_{jx},\end{aligned} \tag{3.19}$$

where

$$\Delta H_{ix} = \sum_y d_{ixy}(H_{iy} - H_{ix}) \text{ and } \Delta P_{jx} = \sum_y d_{jxy}(P_{jy} - P_{jx})$$

are the migration balances of host i at location x and the migration balance of parasite j at location x respectively. However, $d_{ixy} = d/(n-1)$ is the dispersal rate of host and parasite between locations, where n is the number of patches.

We starts with the exchange of dispersers among two populations of one species as an introduction. The following model is a modification of Holt's analysis where d is the propensity to disperse (ie, $0 \leq d \leq 1$) instead of a rate [42]. Following the analysis given by McPeek ([25], p. 228), the simple model

$$\begin{aligned}\frac{dH_{1(1)}}{dt} &= (1-d)\left(r_{1(1)}H_{1(1)} - b_{1(1)}H_{1(1)}^2\right) - dH_{1(1)} + dH_{1(2)} \\ \frac{dH_{1(2)}}{dt} &= (1-d)\left(r_{1(2)}H_{1(2)} - b_{1(2)}H_{1(2)}^2\right) - dH_{1(2)} + dH_{1(1)}\end{aligned}$$

illustrates a number of important possible demographic consequences of dispersal. Dispersal can distort local population abundances away from those favoured by local population regulation and those distortions make abundances more similar across the population ([25], p. 228). Therefore, the greater the propensity (ie, larger d), the closer the local population densities are to one another (as shown in Figure 3.13 below)

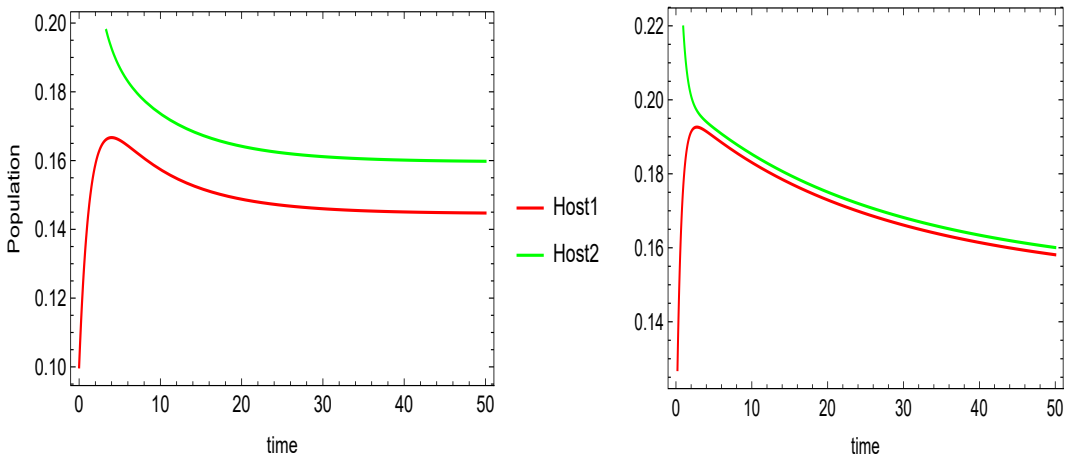

Figure 3.13: The initial conditions are $H_{1(1)}(0) = 0.1$, $H_{1(2)}(0) = 0.3$ and the coefficients have the proportions $r_{1(1)} = 0.1$, $r_{1(2)} = 0.2$, $b_{1(1)} = 1$, $b_{1(2)} = 1$, $e = 0.5$ (**a**) $d = 0.3$, and (**b**) $d = 0.8$.

Holt [43] and Weisser and Hassell [44] studied the effect of dispersal on the stability of a predator-prey system in a single patch and found that this pool of dispersers was always stabilising, and that the stabilising effect was also produced by a pool of dispersing prey. This was extended by Neubert et al. [45] who developed a general way to explicitly account for individual travel times, and show that dispersal is almost always stabilising when an explicit travel time is incorporated in the model. The effect of dispersal on the stability of a predator-prey system in two patches was considered in their study [45]. The simplification which was made is that every patch is identical to every other patch - including being connected via dispersal to the same number at equal distance patches.

3.2.1 Metacommunity matrix

This section explores the main part and contribution of this thesis. The stability criterion of the predator-prey interaction in a metecommunity scale is derived. Recent theoretical work on metacommunities has shown that dispersal by organisms affect patterns of local and regional species diversity, species relative abundances and diversity-productivity relationships in important and non-intuitive ways [24].

To derive the stability criterion, the empirical spectral distribution (ESD) concept was followed. Tao et al. [46] are concerned about the empirical

spectrum distribution convergence of random matrices in both probability and the almost sure sense. They proved the universality phenomenon for the ESD of random matrices and showed that the limiting distribution of the ESD of a random matrix ensemble A_n, depends on the mean and variance of its entries and has independent and identically distributed (iid) entries.

Gravel et al. [1] inherited the results from Tao et al. [46] to compute the support of the ESD of matrix $\mathbf{J} = \mathbf{A} + \mathbf{M}$ of size n, with $\mathbf{A}$ being a random matrix and $\mathbf{M}$ is a deterministic matrix with eigenvalues $m_1, ..., m_n$ using the criterion given by

$$\sigma\sqrt{n} < -m. \tag{3.20}$$

Here, the same theory is used where $\mathbf{A}$ is the predator-prey matrix taken from Allesina and Tang [14] that follows the below algorithm,

Predator-prey algorithm: i) For each pair of interactions $(M_{ij}, M_{ji})_{i>j}$, we draw a random value p_1 from a uniform distribution $U[0,1]$. ii) If $p_1 \leq C$, we draw a second random value p_2 from $U[0,1]$. iii) If $p_2 \leq 0.5$, we draw M_{ij} from a half-normal distribution $|N(0,\sigma^2)|$ and M_{ji} from a negative half-normal $-|N(0,\sigma^2)|$, while if $p_2 > 0.5$ we do the opposite. iv) If $p_1 > C$, we assign 0 to both M_{ij} and M_{ji}. v) All diagonal terms, M_{ii} are set to $-d$. For these matrices. $\bar{\lambda} = -d$ and $\mathrm{Var}(\lambda) = -2(S-1)C\sigma^2/\pi$.

Consider the following Jacobian matrix:

$$\mathbf{J} = \mathbf{A} + \mathbf{M} + \mathbf{D}. \tag{3.21}$$

$\mathbf{M}$ represents the diagonal matrix with values m on the diagonal and 0s in the rest of the matrix, $\mathbf{D}$ is the matrix that represent the effect of dispersal among patches, and $\mathbf{A}$ collects the Jacobian matrices that are arranged as diagonal blocks, which describe the Jacobian matrices that would have arised in isolated communities (except for diagonal terms which are contained in term $\mathbf{M}$). Consecutive blocks of size S describe the stability properties within patches, and the total size of all matrices is $n \times S$ where n is the number of patches.

Assume that the effect of dispersal is diffusive and homogeneous (with diffusion parameter d), then $\mathbf{D}$ can be written as,

$$\mathbf{D} = \begin{bmatrix} -d\mathbf{I} & \frac{d}{n-1}\mathbf{I} & \dots & \frac{d}{n-1}\mathbf{I} \\ \frac{d}{n-1}\mathbf{I} & -d\mathbf{I} & \dots & \frac{d}{n-1}\mathbf{I} \\ \vdots & \frac{d}{n-1}\mathbf{I} & \ddots & \frac{d}{n-1}\mathbf{I} \\ \frac{d}{n-1}\mathbf{I} & \dots & \frac{d}{n-1}\mathbf{I} & -d\mathbf{I} \end{bmatrix}$$

where $\mathbf{I}$ is the identity matrix of size S and also assume that the effects of within-patch interactions on the Jacobian are heterogeneous so that $\mathbf{A}$ can be written as,

$$\mathbf{A} = \begin{bmatrix} A_1 & 0 & \dots & 0 \\ 0 & A_2 & \dots & 0 \\ \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & A_n \end{bmatrix}$$

where the size S of predator-prey matrices $\mathbf{A}$ (with elements a_{ijk}) are independent.

To derive the stability criteria, Allesina and Tang [14] formulated a new conjecture following Sommers et al. [47]. The conjecture states that the eigenvalues of large predator-prey matrices are contained in a vertically stretched ellipse and have mean $-m$ and variance $Var(\lambda) = (S-1)\mathbb{E}(A_{ij}A_{ji})_{i\neq j} = (S-1)C\tau\sigma^2$. Therefore, the corresponding stability criterion for large S of the predator-prey matrix is given by the inequality 3.20 with the appropriate values for parameters b, n and σ as

$$\sigma\tau\sqrt{C\left(1-\frac{1}{S}\right)} \times \sqrt{S} < m, \tag{3.22}$$

where $\tau = 1 - \mathbb{E}^2(|X|)/\sigma^2 = 1 - (\sigma\sqrt{2/\pi})^2/\sigma^2 = 1 - 2/\pi$ since $\mathbb{E}(|X|) = \sigma\sqrt{2/\pi}$.

In the absence of dispersal (ie, $d = 0$), the stability criterion (for large S) of $\mathbf{J} = \mathbf{M} + \mathbf{A}$ is given by inequality 3.22 because the matrix size is of size nS

and the connectance is nC/n^2. For very small d, all eigenvalues are clustered around $-m$, and the first order stability criterion becomes

$$\sigma\tau\sqrt{C(S-1)} < m + d. \tag{3.23}$$

Now, assume that S, n and d are large, then the following stability criterion is obtained:

$$\sigma\tau\sqrt{C(S-1)/n_e} < m, \tag{3.24}$$

where $\tau = (1 - 2/\pi)$ (see Figure. 3.14c and Table 3.3). The effective number of the ecologically independent patches in metacommunity is $n_e = n/[1 + (n-1)\rho]$. When the elements of predator-prey are perfectly correlated among patches (ie, $\rho = 1$), then equation 3.24 simplifies to Allesina and Tang [14] criterion (ie, equation 3.9). When d is small and n, S are large, then the dispersal effect is given by criterion 3.23 (see Figure 3.14b).

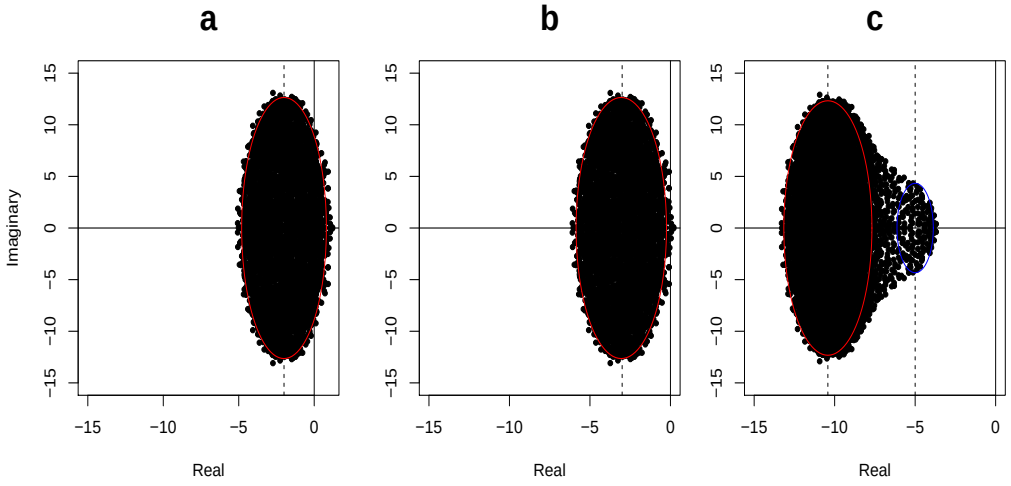

Figure 3.14: Illustration of the eigenvalues distribution in the complex plane. Distribution of the eigenvalues of matrix **J** in the complex plane when $\sigma = 1$, $n_e = n = 20$, $m = 2$, $S = 200$, $C = 0.3$ and (**a**) $d = 0$, (**b**) $d = 1$ and (**c**) $d = 8$.

The table below, summarises the stability criterion relative to Figure 3.14.

Table 3.3: Stability criteria for predator-prey interaction in metacommunity.

Figure	Stability criterion
Figure 3.14a	The radius of eigenvalues in the red ellipse is $\sigma\tau\sqrt{C(S-1)}$, centred around $-m$.
Figure 3.14b	The radius is $\sigma\tau\sqrt{C(S-1)}$, centred around $-(m+d)$.
Figure 3.14c	There is a large subset of the real parts of eigenvalues contained in a distribution with a radius of $\sigma\tau\sqrt{C(S-1)(n-1)/n}$, centred at $-m-\frac{nd}{(n-1)}$ while the remaining eigenvalues are enclosed in a blue distribution of radius $\sigma\tau\sqrt{C(S-1)/n_e}$ centred around $-m$.

Furthermore, the effect of density dependence on the stability of predator-prey matrix in metacommunity is considered. The matrix is explored the same way as in local community. The Jacobian matrix is reconstructed from equation 3.21 as follows,

$$\mathbf{J} = \mathbf{X}(\mathbf{A} + \mathbf{M}) + \mathbf{D}, \tag{3.25}$$

where $\mathbf{X}$ is a diagonal matrix with $X_{ii} = x_i^*$ and zeros elsewhere. The stability criterion for this system is also remain an unsolved and open problem but simulation shows the effect of matrix $\mathbf{X}$ (see Figure 3.15).

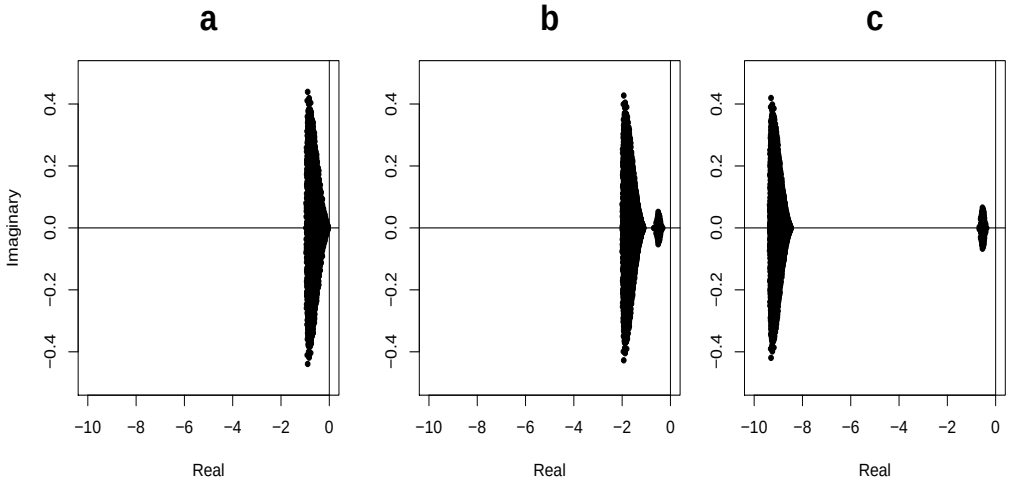

Figure 3.15: Distribution of eigenvalues of the matrix **J** 3.25 in the complex plane when $\sigma = 1/\sqrt{S}, n = 20, S = 200, C = 0.1, m = 1,$, (**a**) $d = 0$, (**b**)$(d = 1)$, and (**c**) $d = 8$. The diagonal entries of density dependense X are sampled from a uniform distribution on [0.05,1]

Figure 3.15 above shows how density dependence affect metacommunity of the predator-prey matrix as dispersal increases. The simulation provides a visual illustration that density dependence stabilise the system.

3.2.2 Generating a metacommunity matrix for bipartite interaction model

In this section, a metacommunity concept is explored considering a bipartite model 3.19. The matricial form of the metacommunity of a bipartite model interaction is given by

$$\begin{aligned} \dot{H} &= H(r - BP) + DH \\ \dot{P} &= P(-q + EB^T H) + DP. \end{aligned} \tag{3.26}$$

This can be combined into a single equation written as

$$\dot{N} = diag(N)(R + AN) + DN. \tag{3.27}$$

The Jacobian matrices are obtained by linearising the system of equations, ie, the Jacobian matrix **J** of metacommunity is expressed as

$$\mathbf{J} = \mathbf{M} + \mathbf{D}, \text{ and } \mathbf{M} = diag(N^*)\mathbf{A} \tag{3.28}$$

where $\mathbf{M}$ collects the local Jacobian matrices 3.18, arranged as diagonal blocks with 0s in the rest of the matrix, $\mathbf{D}$ is the matrix representing the dispersal effect among patches. The total size of all matrices is $n \times S$ where n is the number of patches. Assuming that the effect of dispersal is diffusive and homogeneous (with diffusion parameter d) and that the effects of within-patch interactions on the Jacobian are heterogeneous, matrix $\mathbf{J}$ can be written as:

$$\mathbf{J} = \begin{bmatrix} \mathbf{M}_1 & \mathbf{0} & \dots & \mathbf{0} \\ \mathbf{0} & \mathbf{M}_2 & \dots & \mathbf{0} \\ \vdots & \vdots & \ddots & \vdots \\ \mathbf{0} & \mathbf{0} & \dots & \mathbf{M}_n \end{bmatrix} + \begin{bmatrix} -d\mathbf{I} & \frac{d}{n-1}\mathbf{I} & \dots & \frac{d}{n-1}\mathbf{I} \\ \frac{d}{n-1}\mathbf{I} & -d\mathbf{I} & \dots & \frac{d}{n-1}\mathbf{I} \\ \vdots & \frac{d}{n-1}\mathbf{I} & \ddots & \frac{d}{n-1}\mathbf{I} \\ \frac{d}{n-1}\mathbf{I} & \dots & \frac{d}{n-1}\mathbf{I} & -d\mathbf{I} \end{bmatrix}$$

Figure 3.16 and 3.17 illustrate eigenvalues distribution in the complex plane for metacommunity of a realistic bipartite matrix. In both figures, density dependence is considered. Note that Stone's [33] method is considered for a large matrix in Figure 3.17. This shows that density dependence and dispersal stabilises metacommunity of the bipartite interactions.

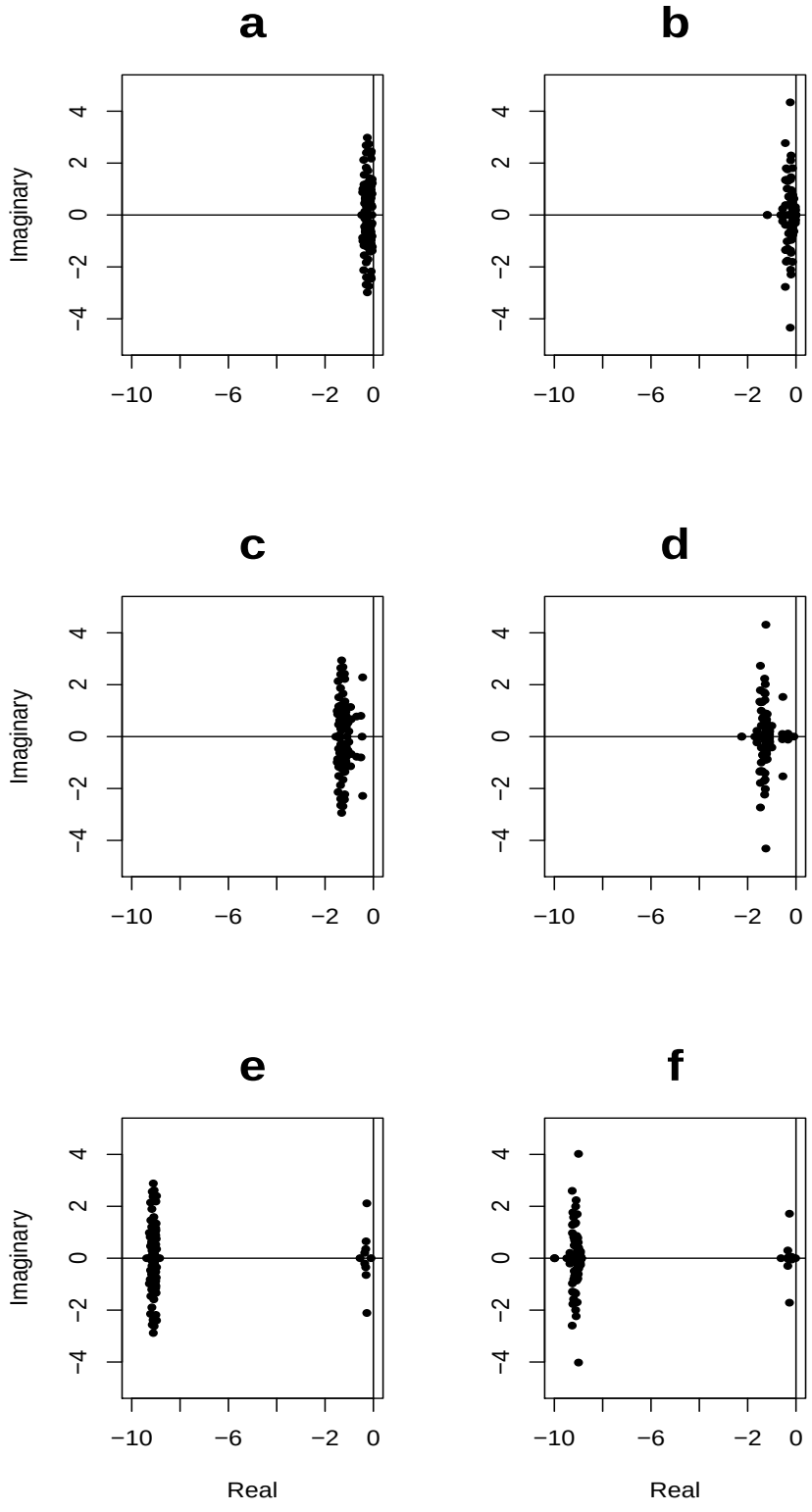

Figure 3.16: Illustration of the eigenvalues distribution in the complex plane. Eigenvalues distribution of matrix $\mathbf{J} = \mathbf{A} + \mathbf{D}$ and matrix $\mathbf{J} = \mathbf{M} + \mathbf{D}$ where $\mathbf{M} = diag(\mathbf{N}^*)\mathbf{A}$ and $\mathbf{N}^* = -(\mathbf{A}^{-1})\mathbf{R}$ in the complex plane when $S = 5$, $n = 10$, $\sigma = 1$, $c = 1$, $e = 0.5$, (**a**) (**b**) $d = 0$, (**c**) (**d**) $d = 1$, and (**e**) (**f**) $d = 8$.

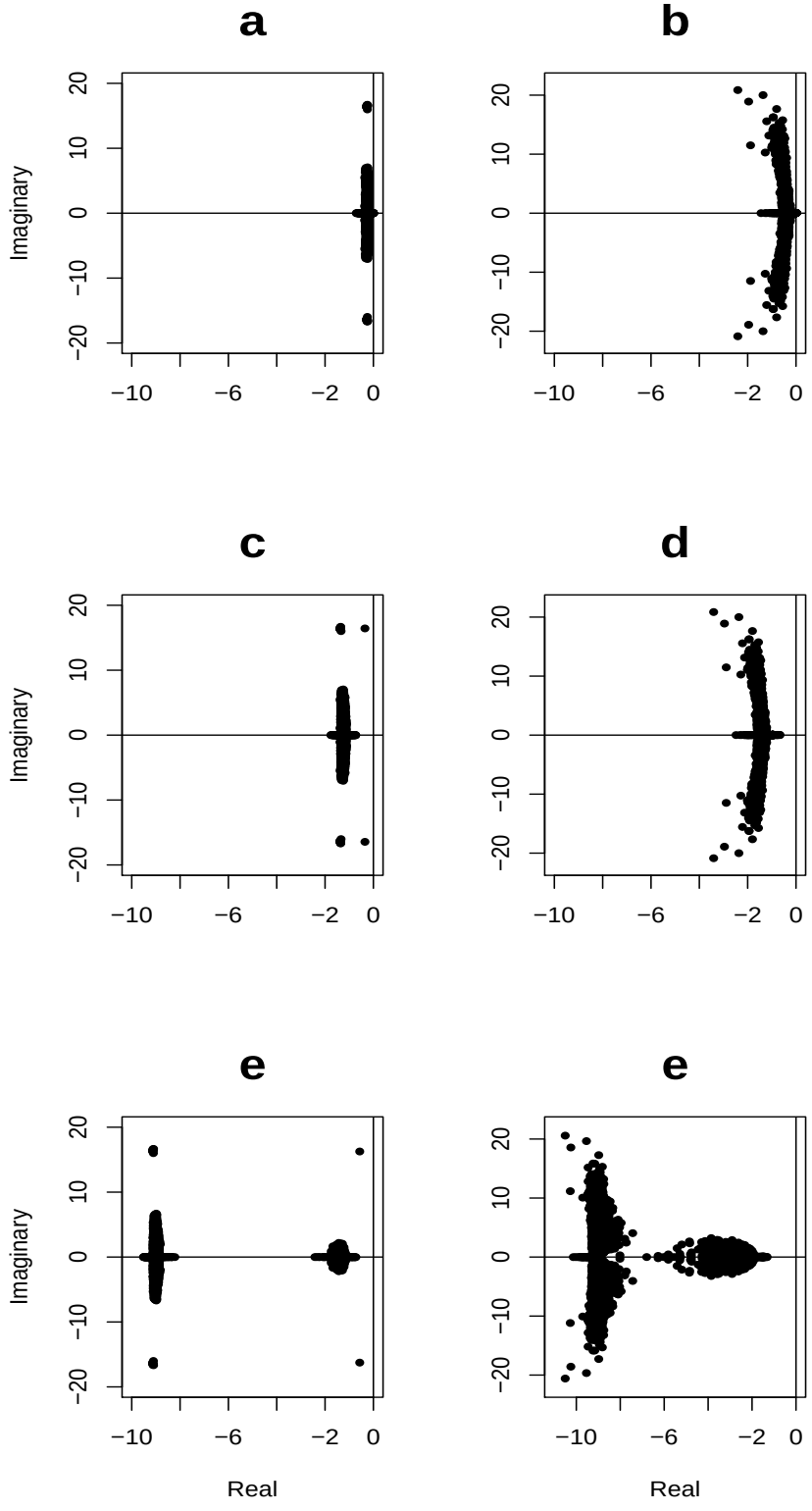

Figure 3.17: Illustration of the eigenvalues distribution in the complex plane. Eigenvalues distribution of the matrix $\mathbf{J} = \mathbf{A} + \mathbf{D}$ and matrix $\mathbf{J} = \mathbf{M} + \mathbf{D}$ where $\mathbf{M} = \mathbf{N}^*\mathbf{A}$ and $\mathbf{N}^*$ is a positive diagonal matrix that is distributed from log-normal distribution in the complex plane when $S = 100$, $n = 10$, $\sigma = 1$, $c = 0.3$, $e = 0.5$, (**a**) (**b**) $d = 0$, (**c**) (**d**) $d = 1$, and (**e**) (**f**) $d = 8$.

3.3 Numerical simulations

In this section, the numerical simulation results of the dispersal effect on stability for Gravel et al. [1] random interaction, are compared with predator-prey and bipartite interaction for the largest real part of the eigenvalue. An illustrative result for the effect of diffusion rate for an average of 100 random metaecosystems of 10 patches and 15 species from Gravel et al. [1] is shown in the Figure 3.18 below.

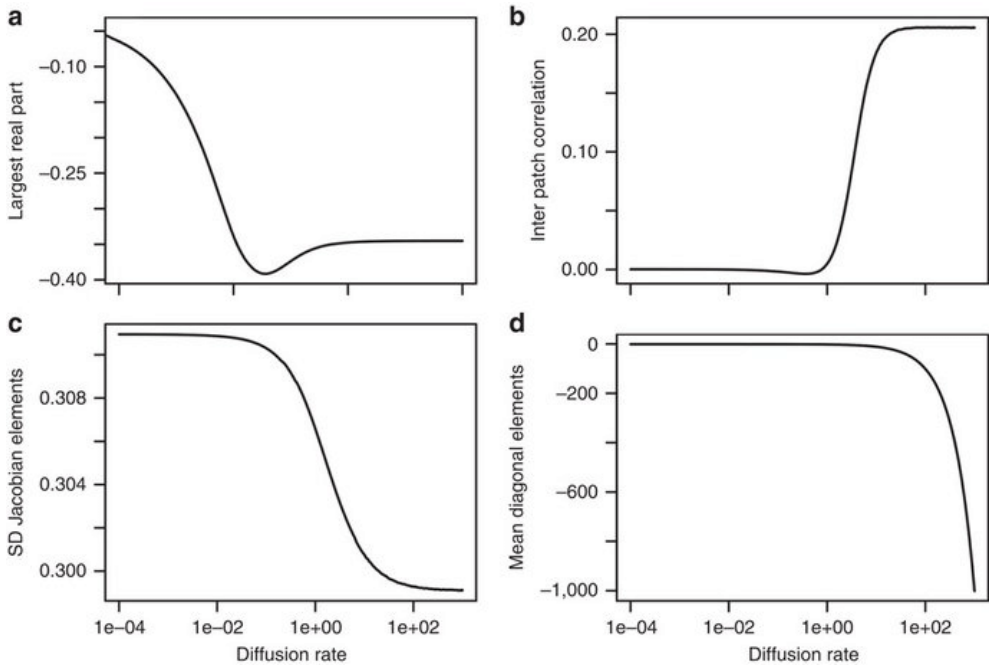

Figure 3.18: Effect of diffusion rate on Jacobian matrices and their stability: (a) The real part of the largest eigenvalue, (b) the s.d. of non-null elements of the Jacobian matrix, (c) inter-patch correlation and (d) mean of the diagonal elements. Metaecosystems were generated randomly with the constraint that all populations have positive equilibrium densities. Each line represents the average of 100 replicated random metaecosystems with increasing diffusion rate. Figure taken directly from Gravel et al. [1].

They found that stability increases with dispersal, peak at intermediate rates, drops and become almost insensitive to high levels [1]. Figure 3.19 illustrate the numerical simulation of the effect of diffusion rate on Jacobian matrices of the predator-prey (**a, b**) and bipartite interaction (**c, d**). Each line represent an average of 100 predator-prey and bipartite metacommunity of 15

species and 10 patches with increasing diffusion rate. When density dependence is considered (**b, d**), stability increase with dispersal, peaking and immediately become insensitive at high rates of dispersal.

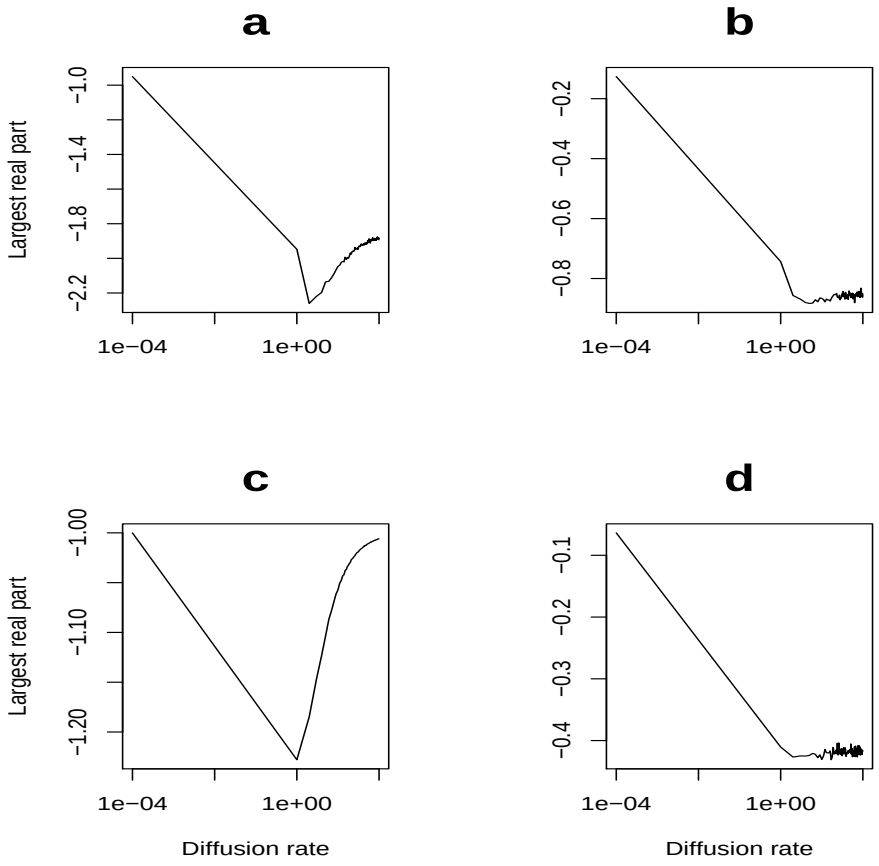

Figure 3.19: The diffusion rate (d) on Jacobian matrices and their stability: The real part of the largest eigenvalue with increasing diffusion rate for Jacobian of predator-prey metacommunity (**a**) without, (**b**) with all density dependence and for Jacobian of bipartite metacommunity (**c**) without and (**d**) with all density dependence.

Dispersal and density dependence affect resilience of the antagonistic communities, ie, how readily antagonistic communities returns to equilibrium after being disturbed. Therefore, the results obtained from Gravel et al. [1] for random metacommunity and those for antagonistic metacommunity in this thesis (Figure 3.19), shows that the antagonistic communities are more stable than community species interacting at random.

Chapter 4

Holling type II functional response

In this chapter, a type II functional response on the bipartite model 3.1 is explored. This is considered as a more realistic concept of the model. The type II functional response is commonly known as the function relating to the number of prey eaten or killed by an average predator per unit time [48]. The time taken by predators to find, kill and consume preys play a fundamental role in shaping trophic interactions [49]. This time is called the handling time.

4.1 Bipartite community with Holling type II

Below is the general bipartite model with type II functional response which is modified from model 3.1 in chapter 3,

$$\frac{dH_i}{dt} = H_i \left(r_i - \sum_{j=1}^{S_p} \frac{b_{ij} P_j}{1 + T \sum_{i=1}^{S_h} b_{ij} H_i} \right) \tag{4.1}$$

$$\frac{dP_j}{dt} = P_j \left(-q_j + \sum_{i=1}^{S_h} \frac{e_{ij} b_{ij} H_i}{1 + T \sum_{i=1}^{S_h} b_{ij} H_i} \right),$$

where T is the handling time, ie, time required by the predator to handle before it is again ready to search for another prey. Oaten and Murdoch

[50] suggested a criterion for which a functional response can be said to be stabilising or not at a particular point. The criterion is given by

$$f'(H) > \frac{f(H)}{H}, \tag{4.2}$$

where $\frac{f(H)}{H}$ represents the proportion of prey killed per unit time per predator. This criterion was constructed without reference to a complete and fully specified mathematical model [48]. If the functional response f satisfies equation 4.1, then f is stabilising at prey population H [50].

Here, one host-one parasite model is constructed from model 4.1 as follows

$$\begin{aligned} \frac{dH}{dt} &= rH\left(1-\frac{H}{K}\right) - \frac{bHP}{1+bTH} \\ \frac{dP}{dt} &= -qP + \frac{ebHP}{1+bTH}. \end{aligned} \tag{4.3}$$

This model is known as the Rosenzweig-MacArthur predator-prey model. Note that this model has been explored widely in the literature, however, this serve as an introduction before exploring functional response in few species and in a community matrix. Rosenzweig-MacArchur model is one of the mechanistic model to explore the ecological and evolotionary dynamics of a community because ([25], p. 28):

1. Many different mechanistic features of species interactions can be incorporated into this basic model.

2. Multiple species can be explicitly modelled in relatively complex webs of interactions.

3. It describes the dynamics of average fitness for each species in the interaction web.

Determining the equilibrium points of the Rosenzweig-MacArchur model 4.3, the equilibrium point of interest is given by

$(H^*, P^*) = \left(\frac{q}{b(e-Tq)}, \frac{er(beK-q-bTKq)}{b^2K(e-Tq)^2}\right)$ which exists when $bK(e-Tq) > q$ and $e > Tq$. Eigenvalues of this model are complicated to be computed. However using Mathematica, the real part of the eigenvalues is given by

$$Re(\lambda) = \frac{1}{2}\left(r + \frac{b(eH^*(1+bH^*T) - P^*)}{(1+bH^*T)^2} - q - \frac{2H^*r}{K}\right). \tag{4.4}$$

Therefore, if $Re(\lambda) < 0$ then the system is stable. From the above equation, if the handling time $T = 0$, then the equation reduces to equation 3.3 in chapter 3. This criterion shows the effect of handling time on the Rosenzweig-MacArthur model (see Figure 4.1).

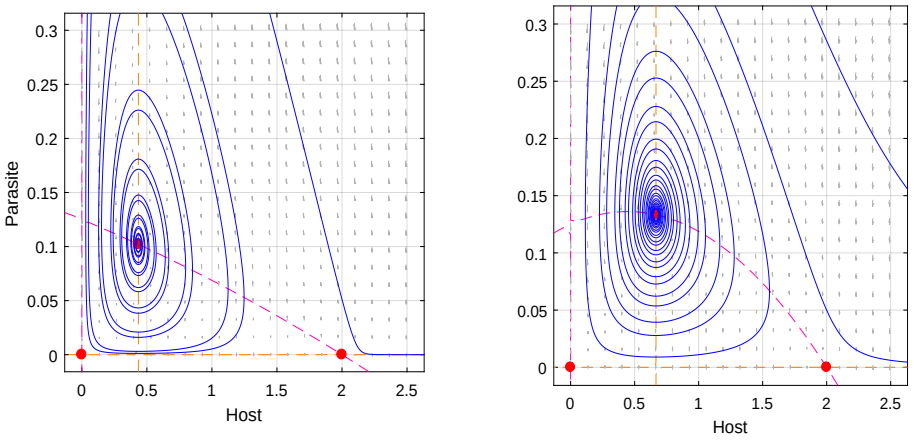

Figure 4.1: Phase portrait for Rosenzweig-MacArthur host-parasite when $r = 0.2$, $K = 2$, $b = 0.8$, $e = 0.6$, $q = 0.2$, $T = 0.1$ on the left panel and $T = 0.9$ on the right panel.

The number of the parameters of model 4.3 can be reduced to

$$\begin{aligned}\frac{dH}{dt} &= rH\left(1 - \frac{H}{K}\right) - Pf(H)\\ \frac{dP}{dt} &= -qP + ePf(H),\end{aligned}$$

where $f(H) = \frac{bH}{1+bTH}$. The equilibrium point is then given by $(f(H^*), P^*) = \left(\frac{q}{e}, \frac{-eH^{*2}r + eH^*Kr}{qK}\right)$. This exist when $-eH^{*2}r + eH^*Kr > 0 \Rightarrow K > H^*$. Determining its eigenvalues gives $\lambda_1 = ef(H^*) - q$ and $\lambda_2 = r\left(1 - \frac{2H^*}{K}\right)$. This system turns to be stable if $ef(H^*) - q < 0 \Rightarrow \frac{q}{e} < f(H^*)$ and $r(1 - \frac{2H^*}{K}) < 0 \Rightarrow 1 < \frac{2H^*}{K}$ provided $K > H^*$. If $K > 2H^*$, then the system becomes unstable

The Rosenzweig-MacArthur model 4.3 can further be written in a nondimensional form by letting

$$H = x/X, \quad P = y/Y$$

where $X, Y > 0$ are determined and arrive at new differential equations for H and$P$, that is

$$H' = \frac{x'}{X} = rH\left(1 - \frac{HX}{K}\right) - \frac{bHPY}{1 + bTHX}$$

and

$$P' = \frac{y'}{Y} = \frac{ebHPX}{1 + bTHX} - qP$$

choosing X, Y so that

$$bT = 1, \quad Y = eX$$

and setting $m = \frac{b}{T}$ and $k = K/X$ then the system becomes

$$H' = rH\left(1 - \frac{H}{k}\right) - \frac{mHP}{1 + H}$$
$$P' = \frac{mHP}{1 + H} - qP$$

finally, by scaling time to be $t = rb$ and using the chain rule $\frac{dH}{db} = \frac{dH}{dt}\frac{dt}{db} = r\frac{dH}{dt}$ and redefining $\bar{m} = m/r$ and $\bar{\mu} = q/r$, gives

$$\frac{dH}{r} = H\left(1 - \frac{H}{k}\right) - \frac{\bar{m}HP}{1 + H}$$
$$\frac{dP}{r} = \frac{\bar{m}HP}{1 + H} - \bar{\mu}P$$

now, by returning to the original variables x, y and t and drop the bars over m and μ to arrive at the nondimensional form system as

$$x' = x\left(1 - \frac{x}{k}\right) - \frac{mxy}{1 + x}$$
$$y' = \frac{mxy}{1 + x} - \mu y.$$

This nondimensional form perspective can also be used to construct a two host-one parasite system below

$$\begin{aligned}
\frac{dH_1}{dt} &= r_1 H_1 \left(1 - \frac{H_1}{K_1}\right) - \frac{b_1 H_1 P}{1 + T(b_1 H_1 + b_2 H_2)} \\
\frac{dH_2}{dt} &= r_2 H_2 \left(1 - \frac{H_2}{K_2}\right) - \frac{b_2 H_2 P}{1 + T(b_1 H_1 + b_2 H_2)} \\
\frac{dP}{dt} &= P\left(\frac{e a_1 H_1}{1 + T(b_1 H_1 + b_2 H_2)} + \frac{e b_2 H_2}{1 + T(b_1 H_1 + b_2 H_2)} - q\right),
\end{aligned} \tag{4.5}$$

as a system given by

$$\begin{aligned}
\frac{dx}{dt} &= x\left(1 - \frac{x}{k_1}\right) - \frac{m_1 x z}{1 + x + y} \\
\frac{dy}{dt} &= y\left(1 - \frac{y}{k_2}\right) - \frac{m_1 y z}{1 + x + y} \\
\frac{dz}{dt} &= z\left(\frac{m_1 x + m_1 y}{1 + x + y} - \mu\right).
\end{aligned}$$

The equilibrium and eigenvalues for this system are complicated to be computed analytically, however, the simulation is computed. Figure 4.2 shows that one parasie goes extinct.

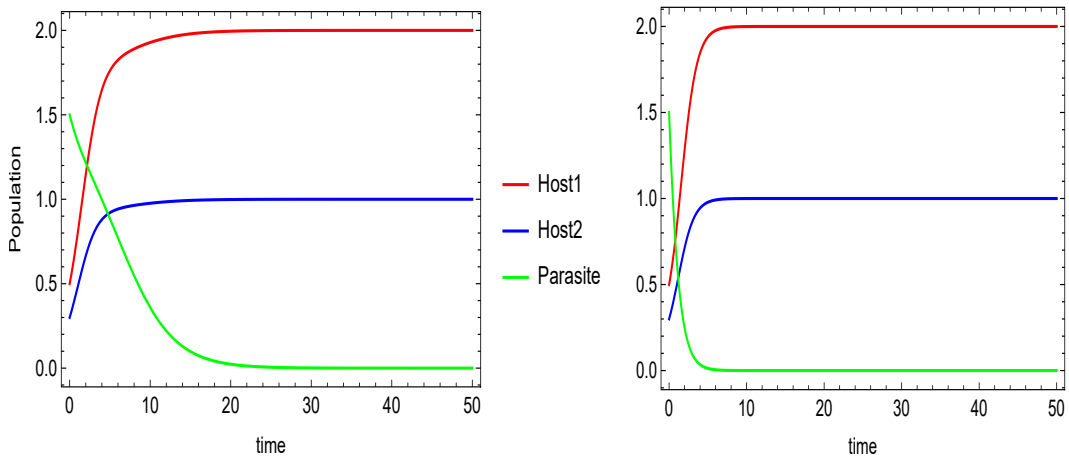

Figure 4.2: Simulation system of a two host-one parasite. The initial conditions are $x(0) = 0.5$, $y(0) = 0.3$, $z(0) = 1.5$, the coefficients have the proportions $k_1 = 2$, $k_2 = 1$, $m_1 = 0.3$, $m_2 = 0.2$, $\mu_1 = 0.3$ on the left panel and $\mu_2 = 1$ on the right panel.

Rosenzweig-MacArthur model is known to have three stability behaviours, ie, parasite extinction, host-parasite stable coexistence and host-parasite periodic coexistence (unstable focus and stable limit cycle).

4.1.1 Eigenvalues distribution in a complex plane for Rosenzweig-MacArthur nonlinear system

In this section, simulations for the eigenvalues distribution in a complex plane for a one host-one parasite (see Figure 4.3) and a three host-two parasite (see Figure 4.4) are considered. This shows how handling time affect the leading eigenvalue of each system.

4.1.1.1 One host-one parasite (2x2 Jacobian matrix)

The system is given by

$$\begin{aligned} \frac{dH}{dt} &= rH\left(1-\frac{H}{K}\right)-\frac{bHP}{1+bTH} \\ \frac{dP}{dt} &= -qP+\frac{ebHP}{1+bTH}, \end{aligned} \tag{4.6}$$

and its Jacobian matrix is given by

$$J = \begin{bmatrix} \frac{\partial \dot{H}}{\partial H} & \frac{\partial \dot{H}}{\partial P} \\ \frac{\partial \dot{P}}{\partial H} & \frac{\partial \dot{P}}{\partial P} \end{bmatrix} = \begin{bmatrix} r(1-\frac{2H^*}{K}) - \frac{bP^*}{1+bTH^*} + \frac{b^2TH^*P^*}{(1+bTH^*)^2} & -\frac{bH^*}{1+bTH^*} \\ \frac{ebP^*}{1+bTH^*} - \frac{eb^2TH^*P^*}{(1+bTH^*)^2} & \frac{ebH^*}{1+bTH^*} - q \end{bmatrix}$$

$$= \begin{bmatrix} r & 0 \\ 0 & -q \end{bmatrix} + \begin{bmatrix} -\frac{2rH^*}{K} - \frac{bP^*}{1+bTH^*} + \frac{b^2TH^*P^*}{(1+bTH^*)^2} & -\frac{bH^*}{1+bTH^*} \\ \frac{ebP^*}{1+bTH^*} - \frac{eb^2TH^*P^*}{(1+bTH^*)^2} & \frac{ebH^*}{1+bTH^*} \end{bmatrix}.$$

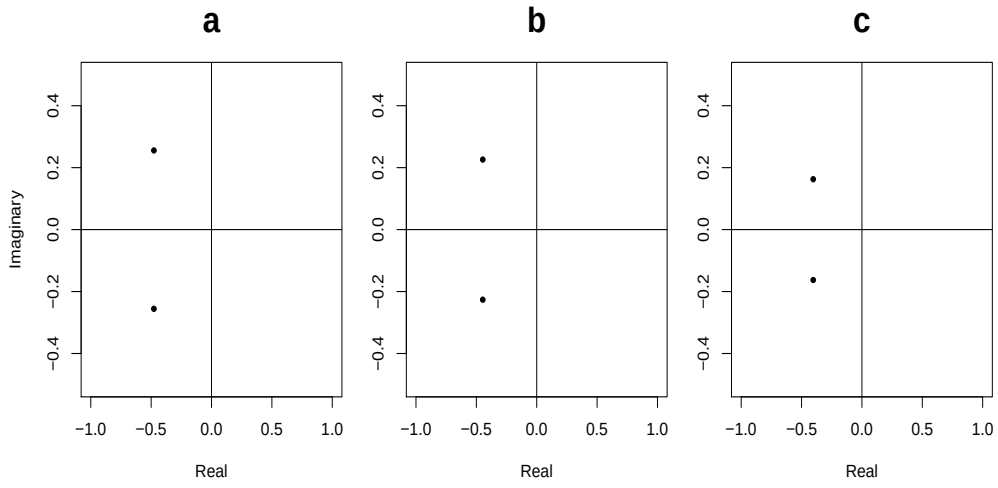

Figure 4.3: Illustration of the eigenvalues distribution in the complex plane. Distribution of the eigenvalues for a one host-one parasite Jacobian matrix **J** when $r = 0.2$, $q = 0.6$, $e = 0.5$, $K = 3$, b follows random distribution, H^*, P^* follows log-normal distribution where (**a**) $T = 0$, (**b**) $T = 0.3$ and (**c**) $T = 0.9$.

4.1.1.2 Three host-two parasite (5x5 Jacobian matrix)

The system is given by

$$\frac{dH_1}{dt} = r_1 H_1\left(1-\frac{H_1}{K_1}\right) - \frac{b_{11}H_1P_1}{1+T(b_{11}H_1+b_{21}H_2+b_{31}H_3)} - \frac{b_{12}H_1P_2}{1+T(b_{12}H_1+b_{22}H_2+b_{32}H_3)}$$

$$\frac{dH_2}{dt} = r_2 H_2\left(1-\frac{H_2}{K_2}\right) - \frac{b_{21}H_2P_1}{1+T(b_{11}H_1+b_{21}H_2+b_{31}H_3)} - \frac{b_{22}H_2P_2}{1+T(b_{12}H_1+b_{22}H_2+b_{32}H_3)}$$

$$\frac{dH_3}{dt} = r_3 H_3\left(1-\frac{H_3}{K_3}\right) - \frac{b_{31}H_3P_1}{1+T(b_{11}H_1+b_{21}H_2+b_{31}H_3)} - \frac{b_{32}H_3P_2}{1+T(b_{12}H_1+b_{22}H_2+b_{32}H_3)}$$

$$\frac{dP_1}{dt} = -q_1P_1 + \frac{eb_{11}H_1P_1+eb_{21}H_2P_1+eb_{31}H_3P_1}{1+T(b_{11}H_1+b_{21}H_2+b_{31}H_3)}$$

$$\frac{dP_2}{dt} = -q_2P_2 + \frac{eb_{12}H_1P_2+eb_{22}H_2P_2+eb_{32}H_3P_2}{1+T(b_{12}H_1+b_{22}H_2+b_{32}H_3)}.$$

The Jacobian matrix for this model is computed analytically using Mathematica.

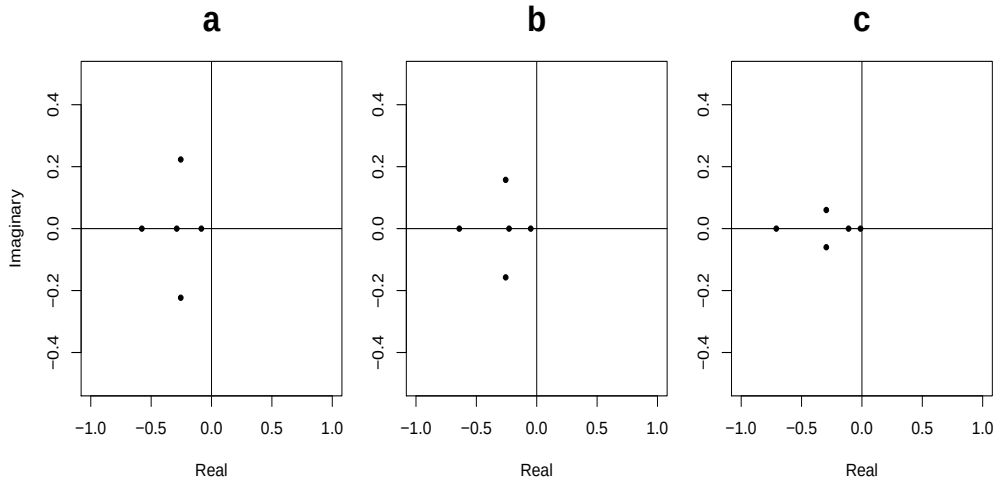

Figure 4.4: Illustration of the eigenvalues distribution in the complex plane. Distribution of the eigenvalues for a three host-two parasite Jacobian matrix **J** when $r_1 = 0.1, r_2 = 0.2, r_3 = 0.15,\ q_1 = 0.6, q_2 = 0.9,\ e = 0.5,\ K = 5,$ $b_{11}, b_{12}, b_{21}, b_{22}, b_{31}, b_{32}$ follows random distribution, $H_1^*, H_2^*, H_3^*, P_1^*, P_2^*$ follows log-normal distribution where (**a**) $T = 0$, (**b**) $T = 0.3$ and (**c**) $T = 0.9$.

When handling time increases, the leading eigenvalues of both systems of a one host-one parasite and a three host-two parasite moves towards the positive side of the complex plane. This shows that the Holling type II functional response destabilises the equilibrium point of a Lotka-Volterra host-parasite model.

4.1.2 Generating a community matrix with Holling type II

Here, a general community matrix for two trophic levels with multiple host-parasite interactions is generated as follows

$$\frac{d\dot{H}}{dt} = H\left(r(1-\frac{H}{K}) - \frac{BP}{1+BH}\right) \tag{4.7}$$

$$\frac{d\dot{P}}{dt} = P\left(-q + \frac{EB^TH}{1+BH}\right).$$

This can be combined and written as the population change rates as described by per-capita change rate times the abundance of the population given by

$$\frac{d\dot{N}}{dt} = Nf(N), \tag{4.8}$$

where $f(N)$ is written as

$$f(N) = \begin{bmatrix} \mathbf{r} & \mathbf{0} \\ \\ \mathbf{0} & -\mathbf{q} \end{bmatrix} + \begin{bmatrix} -\frac{\mathbf{r}\,\mathbf{H}}{\mathbf{K}} & -\frac{\mathbf{B}\,\mathbf{P}}{1+\mathbf{B}\mathbf{H}} \\ \\ \frac{\mathbf{E}\mathbf{B}^{\mathbf{T}}\mathbf{H}}{1+\mathbf{B}\mathbf{H}} & \mathbf{0} \end{bmatrix}$$

$$= \begin{bmatrix} r_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & \ddots & 0 & 0 & 0 & 0 \\ 0 & 0 & r_{S_h} & 0 & 0 & 0 \\ 0 & 0 & 0 & -q_1 & 0 & 0 \\ 0 & 0 & 0 & 0 & \ddots & 0 \\ 0 & 0 & 0 & 0 & 0 & -q_{S_p} \end{bmatrix} + \begin{bmatrix} -\frac{r_1 H_1}{K_1} & \cdots & 0 & -\frac{b_{11}P_1}{1+\sum_{i=1}^{S_h} b_{11}TH_i} & \cdots & -\frac{b_{1S_p}P_{S_p}}{1+\sum_{i=1}^{S_h} b_{1S_p}TH_i} \\ \vdots & \ddots & \vdots & \vdots & \ddots & \vdots \\ 0 & \cdots & -\frac{r_{S_h}H_{S_h}}{K_i} & -\frac{b_{S_h1}P_1}{1+\sum_{i=1}^{S_h} b_{S_h1}TH_i} & \cdots & -\frac{b_{S_hS_p}P_{S_p}}{1+\sum_{i=1}^{S_h} b_{S_hS_p}TH_i} \\ \frac{eb_{11}H_1}{1+\sum_{i=1}^{S_h} b_{11}TH_i} & \cdots & \frac{eb_{S_h1}S_h}{1+\sum_{i=1}^{S_h} b_{S_h1}TH_i} & 0 & \cdots & 0 \\ \vdots & \ddots & \vdots & \vdots & \ddots & \vdots \\ \frac{eb_{1S_p}H_1}{1+\sum_{i=1}^{S_h} b_{1S_p}TH_i} & \cdots & \frac{eb_{S_hS_p}S_h}{1+\sum_{i=1}^{S_h} b_{S_hS_p}TH_i} & 0 & \cdots & 0 \end{bmatrix}.$$

At equilibrium N^*, the community matrix of equation 4.8 simplifies to

$$\frac{d\dot{N}}{dt} = diag(N^*)f'(N^*)$$

$$= \begin{pmatrix} \begin{bmatrix} H_1^* & 0 & 0 & 0 & 0 & 0 \\ 0 & \ddots & 0 & 0 & 0 & 0 \\ 0 & 0 & H_{S_h}^* & 0 & 0 & 0 \\ 0 & 0 & 0 & P_1^* & 0 & 0 \\ 0 & 0 & 0 & 0 & \ddots & 0 \\ 0 & 0 & 0 & 0 & 0 & P_{S_p}^* \end{bmatrix} \end{pmatrix} \begin{pmatrix} \begin{bmatrix} \frac{b_{11}^2 P_1^*}{W_1^2} + \ldots + \frac{b_{1S_p}^2 P_{S_p}^*}{W_{S_p}^2} - \frac{r_1}{K_1} & \cdots & \frac{b_{11} b_{S_h 1} T P_1^*}{W_1^2} + \ldots + \frac{b_{1S_p} b_{S_h S_p} T P_{S_p}^*}{W_{S_p}^2} & -\frac{b_{11}}{W_1} & \cdots & -\frac{b_{1S_p}}{W_{S_p}} \\ \vdots & \ddots & \vdots & \vdots & \ddots & \vdots \\ \frac{b_{11} b_{S_h 1} T P_1^*}{W_1^2} + \ldots + \frac{b_{1S_p} b_{S_h S_p} T P_{S_p}^*}{W_i^2} & \cdots & \frac{b_{S_h 1}^2 P_1^*}{W_1^2} + \ldots + \frac{b_{S_h S_p}^2 P_{S_p}^*}{W_{S_p}^2} - \frac{r_{S_h}}{K_i} & -\frac{b_{S_h 1}}{W_1} & \cdots & -\frac{b_{S_h S_p}}{W_{S_p}} \\ \frac{eb_{11}}{W_1} - \frac{eb_{11}^2 H_1^* - \ldots - eb_{11} b_{S_h 1} T H_{S_h}^*}{W_1^2} & \cdots & \frac{eb_{S_h 1}}{W_1} - \frac{eb_{S_h 1}^2 H_{S_h}^* - \ldots - eb_{11} b_{S_h 1} T H_1^*}{W_1^2} & 0 & \cdots & 0 \\ \vdots & \ddots & \vdots & \vdots & \ddots & \vdots \\ \frac{eb_{1S_p}}{W_{S_p}} - \frac{eb_{1S_p}^2 H_1^* - \ldots - eb_{1S_p} b_{S_h S_p} T H_{S_h}^*}{W_{S_p}} & \cdots & \frac{eb_{S_h S_p}}{W_{S_p}} - \frac{eb_{S_h S_p}^2 H_{S_h}^* - \ldots - eb_{1S_p} b_{S_h S_p} T H_1^*}{W_{S_p}} & 0 & \cdots & 0 \end{bmatrix} \end{pmatrix},$$

where $W_j = 1 + \sum_{i=1}^{S_h} b_{ij} T H_i$.

The generated Jacobian matrix $\frac{d\dot{N}}{dt}$ is used to determine the simulation for the effect of Holling type II functional response with multiple species. Figure 4.5 illustrate the effect of handling time T on the bipartite community matrix.

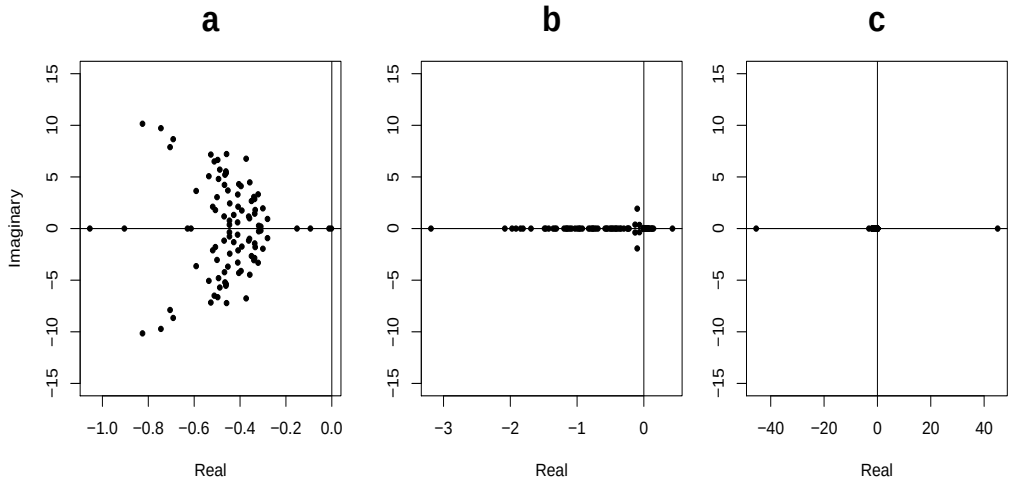

Figure 4.5: Illustration of the eigenvalues distribution in the complex plane. Distribution of the eigenvalues of matrix $d\dot{N}/dN$ in the complex plane when $\sigma = 1$, $S = 50$, $C = 0.3$, $e = 0.3$ and (**a**) $T = 0$, (**b**) $T = 0.3$ and (**c**) $T = 0.8$.

The type II functional response destabilises the bipartite community matrix. The leading eigenvalue of the system is moving towards the positive side of the complex plane as handling time T increases (see Figure 4.5b and 4.5c).

Chapter 5

Concluding remarks

5.1 Conclusion

My analysis shows that large antagonistic interactions in metacommunity are stabilising. The contribution of this thesis is that antagonistic metacommunities are more stable than communities interacting at rondom. The stability criterion for predator-prey metacommunity was obtained in chapter 3 equation 3.24. Furthermore, Figure 3.14 shows how dispersal stabilises this system. For a more realistic bipartite interactions, dispersal stabilises the system structure. However, the shape of eigenvalues distributed is different compared to the predator-prey ellipse shape.

The density dependence of species also plays an important role as it stabilises both the system of predator-prey and bipartite metacommunities (see Figure 3.15, 3.16 and 3.17). On the basis of numerical simulation, result shows that stability increases with dispersal, peaking at the high rates and immediately become insensitive in both predator-prey and bipartite systems (see Figure 3.19b and 3.19d). In chapter 4, result shows that the function of Holling type II response destabilise the bipartite interaction system. The leading eigenvalue in the complex plane is moving towards the positive when handling time of parasite is high (see Figure 4.3, 4.4 and 4.5).

In general, community interactions should be moderated to ensure stability of the equilibrium. This thesis highlight that metacommunity of predator-prey and more realistic structures are beneficial for stability. Is shows that

spatial dynamics in large metacommunity can be stabilising and facilitate coexistence among many antagonistic interacting species.

The relationship between the modern mathematical models and the natural world complications should be emphasised [32]. In the real world, there are complicated characters of individual interactions between species (eg, spatial heterogeneity and predator switching). These complications are present even when a one or two species system are modelled. [32]. There are also complexities that results upon the inclusion of large numbers of species in communities [32]. Therefore, an understanding of stability must embrace system analysis in ecological systems fully [32]. Haydon [9] asked a question, what properties should ecosystems have to be as stable as mathematically possible? This is an obvious and simple result mathematically, yet it provides a theoretical basis for a number of ecologically interesting speculations [9].

5.2 Future work

Ecologists maintain that non-random structures are a key for stability [52]. This section highlight a future work for a proposed tritrophic interaction model as another major study in this field. This is an extension of a bipartite community model. Below is the modification of the general model for tritrophic interaction that was built from Rosenzweig-MacArthur model of consumer-resource interactions.

$$\frac{dH_i}{dt} = H_i \left(\alpha_i - \sum_{j=1}^{q} \frac{b_{ij} P_{jx}}{1 + \sum_{i=1}^{p} b_{ij} h_{ij} H_i} \right) \tag{5.1}$$

$$\frac{dP_j}{dt} = P_j \left(\sum_{j=1}^{p} \frac{e_{ij} b_{ij} H_i}{1 + \sum_{i=1}^{p} b_{ij} h_{ij} H_i} - \sum_{k=1}^{s} \frac{b_{jk} R_k}{1 + \sum_{j=1}^{q} b_{jk} l_{jk} P_j} - \mu_j \right)$$

$$\frac{dR_k}{dt} = R_k \left(\sum_{j=1}^{q} \frac{\beta_{jk} b_{jk} P_j}{1 + \sum_{j=1}^{q} b_{jk} l_{jk} P_j} - \sigma_k \right).$$

where the variables and parameters are defined in Table 5.1.

Table 5.1: State variable and parameter description for a tritrophic model.

State variable	Description
H_i	Population abundance of host i
i	Subscript indexing host species
p	Total number of host species
P_j	Population abundance of parasite j
j	Subscript indexing parasite species
q	Total number of parasite species
R_k	Population abundance of hyperparasite k
k	Subscript indexing hyperparasite species
s	Total number of hyperparasite species
Parameter	**Description**
α_i	Intrinsic population grow rate of host i
b_{ij}	Attack coefficient of parasite j feeding on host i
e_{ij}	Conversion efficiency for parasite j feeding on host i
h_{ij}	Handling time for parasite j eating host i
a_{jk}	Attack coefficient of hyperparasite k feeding on parasite j
β_{jk}	Conversion efficiency for hyperparasite k feeding on parasite j
l_{jk}	Handling time for hyperparasite k eating parasite j
β_j	Death rate of parasite j
σ_k	Death rate of hyperparasite k

5.2.1 One host-one parasite-one hyperparasite

A generated simple tritrophic submodel from model 5.1 is given by

$$\begin{aligned} \frac{dH}{dt} &= H\left(\alpha - b_1 P\right) \\ \frac{dP}{dt} &= P\left(eb_1 H - b_2 R - \mu\right) \\ \frac{dR}{dt} &= R\left(eb_2 P - \sigma\right). \end{aligned} \tag{5.2}$$

From this system, no equilibrium is possible because the three isoclines can never intersect simultaneously at a single point or line. The hyperparasite cannot invade a system of the host and parasite in a neutral limit cycle. Note that this system is the same as a two host-one parasite case in section 3.1. That means the logistic growth or density dependence is required in at least one species for all species to coexist ([25], p. 49). If parasites are ecologically distinct and hence only two are present together with hyperparasite and host in a diamond-shaped community, then each species will satisfy the invasibility criterion, however this is not true if the parasites are ecologically identical ([25], p. 12-13). This section leaves a space for future studies with multiple species in a community.

Recent studies also showed that stable steady state can be non-reactive (ie, all disturbances immediately decay) or it can be reactive (ie, some disturbances initially increases before decaying). Tang and Allesina [26] derived an analytical criteria of large ecological systems for the reactivity in which species interact randomly. Reactivity is defined as an intermediate state between instability and non-reactivity and it could be used to develop an early warning signal for systems approaching instability [26]. This can be applied into the systems of metacommunities with antagonistic interactions.

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Appendix

```
# R code for metacommunity of predator-prey interactions.

library("plotrix")
library("Matrix")
library("magic")

H_P_meta_community = function(S,C,sg,m,d,n){
  s = S*S       # Total number of species interaction
  nc = round(C*S*(S-1)/2, digits = 0)# Number of connectance

  M1 = matrix(0,S,S);M2 = matrix(0,S,S)
  M3 = matrix(0,S,S);M4 = matrix(0,S,S)
  M5 = matrix(0,S,S);M6 = matrix(0,S,S)
  M7 = matrix(0,S,S);M8 = matrix(0,S,S)
  M9 = matrix(0,S,S);M10= matrix(0,S,S)
  Mab = matrix(0,S,S)

  # Construction of predator-prey matrix following
  # algorithm from Allesina & Tang

  I <- rep(1,S-1)
  J <- 2:S
  for(i in 2:(S-1)){
    I <- c(I,rep(i,S-i))
    J <- c(J,(i+1):S)
  }
```

```
sam <- sample(length(I),nc)
inter <- cbind(I,J)[sam,]

for(i in 1:nc){
  if(runif(1) >0.5){
    M1[inter[i,1],inter[i,2]]<- abs(rnorm(1,0,sg))
    M1[inter[i,2],inter[i,1]]<- -abs(rnorm(1,0,sg))
  }else{
    M1[inter[i,1],inter[i,2]]<- -abs(rnorm(1,0,sg))
    M1[inter[i,2],inter[i,1]]<- abs(rnorm(1,0,sg))
  }
}# end of community 1

for(i in 1:nc){
  if(runif(1) >0.5){
    M2[inter[i,1],inter[i,2]]<- abs(rnorm(1,0,sg))
    M2[inter[i,2],inter[i,1]]<- -abs(rnorm(1,0,sg))
  }else{
    M2[inter[i,1],inter[i,2]]<- -abs(rnorm(1,0,sg))
    M2[inter[i,2],inter[i,1]]<- abs(rnorm(1,0,sg))
  }
}# end of community 2

for(i in 1:nc){
  if(runif(1) >0.5){
    M3[inter[i,1],inter[i,2]]<- abs(rnorm(1,0,sg))
    M3[inter[i,2],inter[i,1]]<- -abs(rnorm(1,0,sg))
  }else{
    M3[inter[i,1],inter[i,2]]<- -abs(rnorm(1,0,sg))
    M3[inter[i,2],inter[i,1]]<- abs(rnorm(1,0,sg))
  }
}# end of community 3

for(i in 1:nc){
  if(runif(1) >0.5){
    M4[inter[i,1],inter[i,2]]<- abs(rnorm(1,0,sg))
```

```
    M4[inter[i,2],inter[i,1]]<- -abs(rnorm(1,0,sg))
  }else{
    M4[inter[i,1],inter[i,2]]<- -abs(rnorm(1,0,sg))
    M4[inter[i,2],inter[i,1]]<- abs(rnorm(1,0,sg))
  }
}# end of community 4

for(i in 1:nc){
  if(runif(1) >0.5){
    M5[inter[i,1],inter[i,2]]<- abs(rnorm(1,0,sg))
    M5[inter[i,2],inter[i,1]]<- -abs(rnorm(1,0,sg))
  }else{
    M5[inter[i,1],inter[i,2]]<- -abs(rnorm(1,0,sg))
    M5[inter[i,2],inter[i,1]]<- abs(rnorm(1,0,sg))
  }
}# end of community 5

for(i in 1:nc){
  if(runif(1) >0.5){
    M6[inter[i,1],inter[i,2]]<- abs(rnorm(1,0,sg))
    M6[inter[i,2],inter[i,1]]<- -abs(rnorm(1,0,sg))
  }else{
    M6[inter[i,1],inter[i,2]]<- -abs(rnorm(1,0,sg))
    M6[inter[i,2],inter[i,1]]<- abs(rnorm(1,0,sg))
  }
}# end of community 6

for(i in 1:nc){
  if(runif(1) >0.5){
    M7[inter[i,1],inter[i,2]]<- abs(rnorm(1,0,sg))
    M7[inter[i,2],inter[i,1]]<- -abs(rnorm(1,0,sg))
  }else{
    M7[inter[i,1],inter[i,2]]<- -abs(rnorm(1,0,sg))
    M7[inter[i,2],inter[i,1]]<- abs(rnorm(1,0,sg))
  }
}# end of community 7
```

```
for(i in 1:nc){
  if(runif(1) >0.5){
    M8[inter[i,1],inter[i,2]]<- abs(rnorm(1,0,sg))
    M8[inter[i,2],inter[i,1]]<- -abs(rnorm(1,0,sg))
  }else{
    M8[inter[i,1],inter[i,2]]<- -abs(rnorm(1,0,sg))
    M8[inter[i,2],inter[i,1]]<- abs(rnorm(1,0,sg))
  }
}# end of community 8

for(i in 1:nc){
  if(runif(1) >0.5){
    M9[inter[i,1],inter[i,2]]<- abs(rnorm(1,0,sg))
    M9[inter[i,2],inter[i,1]]<- -abs(rnorm(1,0,sg))
  }else{
    M9[inter[i,1],inter[i,2]]<- -abs(rnorm(1,0,sg))
    M9[inter[i,2],inter[i,1]]<- abs(rnorm(1,0,sg))
  }
}# end of community 9

for(i in 1:nc){
  if(runif(1) >0.5){
    M10[inter[i,1],inter[i,2]]<- abs(rnorm(1,0,sg))
    M10[inter[i,2],inter[i,1]]<- -abs(rnorm(1,0,sg))
  }else{
    M10[inter[i,1],inter[i,2]]<- -abs(rnorm(1,0,sg))
    M10[inter[i,2],inter[i,1]]<- abs(rnorm(1,0,sg))
  }
}# end of community 10


# Contructing self-interaction matrix

M = diag(-m,S,S)# Diagonal matrix representing intraspecific DD
```

```
s1 = cbind(M,Mab,Mab,Mab,Mab,Mab,Mab,Mab,Mab,Mab)
s2 = cbind(Mab,M,Mab,Mab,Mab,Mab,Mab,Mab,Mab,Mab)
s3 = cbind(Mab,Mab,M,Mab,Mab,Mab,Mab,Mab,Mab,Mab)
s4 = cbind(Mab,Mab,Mab,M,Mab,Mab,Mab,Mab,Mab,Mab)
s5 = cbind(Mab,Mab,Mab,Mab,M,Mab,Mab,Mab,Mab,Mab)
s6 = cbind(Mab,Mab,Mab,Mab,Mab,M,Mab,Mab,Mab,Mab)
s7 = cbind(Mab,Mab,Mab,Mab,Mab,Mab,M,Mab,Mab,Mab)
s8 = cbind(Mab,Mab,Mab,Mab,Mab,Mab,Mab,M,Mab,Mab)
s9 = cbind(Mab,Mab,Mab,Mab,Mab,Mab,Mab,Mab,M,Mab)
s10= cbind(Mab,Mab,Mab,Mab,Mab,Mab,Mab,Mab,Mab,M)


S_int = rbind(s1,s2,s3,s4,s5,s6,s7,s8,s9,s10)

# Constructing predator_prey interaction matrix

m1 = cbind(M1,Mab,Mab,Mab,Mab,Mab,Mab,Mab,Mab,Mab)
m2 = cbind(Mab,M2,Mab,Mab,Mab,Mab,Mab,Mab,Mab,Mab)
m3 = cbind(Mab,Mab,M3,Mab,Mab,Mab,Mab,Mab,Mab,Mab)
m4 = cbind(Mab,Mab,Mab,M4,Mab,Mab,Mab,Mab,Mab,Mab)
m5 = cbind(Mab,Mab,Mab,Mab,M5,Mab,Mab,Mab,Mab,Mab)
m6 = cbind(Mab,Mab,Mab,Mab,Mab,M6,Mab,Mab,Mab,Mab)
m7 = cbind(Mab,Mab,Mab,Mab,Mab,Mab,M7,Mab,Mab,Mab)
m8 = cbind(Mab,Mab,Mab,Mab,Mab,Mab,Mab,M8,Mab,Mab)
m9 = cbind(Mab,Mab,Mab,Mab,Mab,Mab,Mab,Mab,M9,Mab)
m10= cbind(Mab,Mab,Mab,Mab,Mab,Mab,Mab,Mab,Mab,M10)



HP_int = rbind(m1,m2,m3,m4,m5,m6,m7,m8,m9,m10)


# Contructing dispersal matrix following Gravel et al SI

DP = diag(d/(n-1),S,S)  # Diagonal matrix of d/n-1
D = diag(-d,S,S)        # Diagonal matrix of -d
```

```
  d1 = cbind(D,DP,DP,DP,DP,DP,DP,DP,DP,DP)
  d2 = cbind(DP,D,DP,DP,DP,DP,DP,DP,DP,DP)
  d3 = cbind(DP,DP,D,DP,DP,DP,DP,DP,DP,DP)
  d4 = cbind(DP,DP,DP,D,DP,DP,DP,DP,DP,DP)
  d5 = cbind(DP,DP,DP,DP,D,DP,DP,DP,DP,DP)
  d6 = cbind(DP,DP,DP,DP,DP,D,DP,DP,DP,DP)
  d7 = cbind(DP,DP,DP,DP,DP,DP,D,DP,DP,DP)
  d8 = cbind(DP,DP,DP,DP,DP,DP,DP,D,DP,DP)
  d9 = cbind(DP,DP,DP,DP,DP,DP,DP,DP,D,DP)
  d10= cbind(DP,DP,DP,DP,DP,DP,DP,DP,DP,D)



  Dsp = rbind(d1,d2,d3,d4,d5,d6,d7,d8,d9,d10)


  AA = HP_int + S_int + Dsp # Meta_ecosystem of size n*S
}

n  = 20          # Number of patches
sg = 1           #Interspecific interaction strength
C  = 0.3         # Connectance
S  = 200         # Number of species
m  = 2           # Intraspecific interaction
d  = 0           # Dispersal rate


AA = H_P_meta_community(S,C,sg,m,d,n)
E = eigen(AA)$values

pdf("Rplotm.pdf",3,4)
plot(Re(E), Im(E), pch=20, xlim = c(-20,20), ylim = c(-20,20),
     xlab = "Real", ylab = "Imaginary", main = "Predator-prey"
     ,cex.main=1,cex.lab=1,cex.axis=1)
```

```
abline(h=0, lty=1)
abline(v=0, lty=1)
abline(v=-m, lty=2)
a1 = sg*sqrt(C*(S-1)*(n-1)/n)*(1 - 2/pi)
b1 = sg*sqrt(C*(S-1)*(n-1)/n)*(1 + 2/pi)
draw.ellipse(-(m+n*d/(n-1)),0,a1,b1,border = 'red')



# R code for metacommunity od bipartite interactions

library("plotrix")
library("Matrix")
library("magic")
library("fdrtool")
library("matrixcalc")

Bipartite_Generator = function(S,ct,sg,e,d1,d2,n){

  x1=1
  while (x1>0) {

    nc = round(ct*S*S, digits = 0) # Number of connectance species

    B1 = matrix(0,S,S)
    Mab= matrix(0,S,S)


    I <- rep(1,S)
    J <- 1:S
    for(i in 2:(S)){
      I <- c(I,rep(i,S))
      J <- c(J,1:S)
    }
```

```
sam1 <- sample(length(I),nc)
inter1 <- cbind(I,J)[sam1,]
for(i in 1:nc){
  if(runif(1) >0.5){
    B1[inter1[i,1],inter1[i,2]]<- -abs(rnorm(1,0,sg))
  }else{
    B1[inter1[i,2],inter1[i,1]]<- -abs(rnorm(1,0,sg))
  }
}#B1



C1 = -diag(runif(S,0.05,1),S,S)
BB1 = t(abs(B1))
Ep = matrix(e,S,S)

BT1 = Ep*BB1

Bi1 = cbind(C1,B1)
Bj1 = cbind(BT1,Mab)
A1= rbind(Bi1,Bj1)

Dt1 = det(A1)
A.inv1 = solve(A1)

r1 = matrix(rlnorm(S, 0.9, 1),S,1)
q1 = -matrix(rlnorm(S, 0, 0.1),S,1)
R1  = rbind(r1,q1)

N1 = -A.inv1%*%R1
xx1 = x1
if (length(which(N1<0)) == 0) {
  x1 = -1
}else{
  x1 = x1+1}
```

```
  N.Diag1 = diag(as.numeric(N1))

  AA1 = A1
  #AA1 = N.Diag1%*%A1
}
return(AA1)# return 1

x2=1
while (x2>0) {

  nc = round(ct*S*S, digits = 0)    # Number of connectance species

  B2 = matrix(0,S,S)
  Mab= matrix(0,S,S)


  J <- 1:S
  for(i in 2:(S)){
    I <- c(I,rep(i,S))
    J <- c(J,1:S)
  }


  sam2 <- sample(length(I),nc)
  inter2 <- cbind(I,J)[sam2,]
  for(i in 1:nc){
    if(runif(1) >0.5){
      B2[inter2[i,1],inter2[i,2]]<- -abs(rnorm(1,0,sg))
    }else{
      B2[inter2[i,2],inter2[i,1]]<- -abs(rnorm(1,0,sg))
    }
  }#B2



  C2 = -diag(runif(S,0.05,1),S,S)
```

```
  BB2 = t(abs(B2))
  Ep = matrix(e,S,S)

  BT2 = Ep*BB2

  Bi2 = cbind(C2,B2)
  Bj2 = cbind(BT2,Mab)
  A2= rbind(Bi2,Bj2)

  Dt2 = det(A2)
  A.inv2 = solve(A2)

  r2 = matrix(rlnorm(S, 0.9, 1),S,1)
  q2 = -matrix(rlnorm(S, 0, 0.1),S,1)
  R2  = rbind(r2,q2)

  N2 = -A.inv2%*%R2
  xx2 = x2
  if (length(which(N2<0)) == 0) {
    x2 = -1
  }else{
    x2 = x2+1}

  N.Diag2 = diag(as.numeric(N2))

  AA2 = A2
  #AA2 = N.Diag2%*%A2
}
return(AA2)# return 2


x3=1
while (x3>0) {

  nc = round(ct*S*S, digits = 0)    # Number of connectance species
```

```
B3 = matrix(0,S,S)
Mab= matrix(0,S,S)


I <- rep(1,S)
J <- 1:S
for(i in 2:(S)){
  I <- c(I,rep(i,S))
  J <- c(J,1:S)
}


sam3 <- sample(length(I),nc)
inter3 <- cbind(I,J)[sam3,]
for(i in 1:nc){
  if(runif(1) >0.5){
    B3[inter3[i,1],inter3[i,2]]<- -abs(rnorm(1,0,sg))
  }else{
    B3[inter3[i,2],inter3[i,1]]<- -abs(rnorm(1,0,sg))
  }
}#B3



C3 = -diag(runif(S,0.05,1),S,S)
BB3 = t(abs(B3))
Ep = matrix(e,S,S)

BT3 = Ep*BB3

Bi3 = cbind(C3,B3)
Bj3 = cbind(BT3,Mab)
A3= rbind(Bi3,Bj3)

Dt3 = det(A3)
A.inv3 = solve(A3)
```

```
  r3 = matrix(rlnorm(S, 0.9, 1),S,1)
  q3 = -matrix(rlnorm(S, 0, 0.1),S,1)
  R3  = rbind(r3,q3)

  N3 = -A.inv3%*%R3
  xx3 = x3
  if (length(which(N3<0)) == 0) {
    x3 = -1
  }else{
    x3 = x3+1}

  N.Diag3 = diag(as.numeric(N3))

  AA3 = A3
  #AA3 = N.Diag3%*%A3
}
return(AA3)# return 3



x4=1
while (x4>0) {

  nc = round(ct*S*S, digits = 0)    # Number of connectance species

  B4 = matrix(0,S,S)
  Mab= matrix(0,S,S)


  I <- rep(1,S)
  J <- 1:S
  for(i in 2:(S)){
    I <- c(I,rep(i,S))
    J <- c(J,1:S)
  }
```

```
sam4 <- sample(length(I),nc)
inter4 <- cbind(I,J)[sam4,]
for(i in 1:nc){
  if(runif(1) >0.5){
    B4[inter4[i,1],inter4[i,2]]<- -abs(rnorm(1,0,sg))
  }else{
    B4[inter4[i,2],inter4[i,1]]<- -abs(rnorm(1,0,sg))
  }
}#B4



C4 = -diag(runif(S,0.05,1),S,S)
BB4 = t(abs(B4))
Ep = matrix(e,S,S)

BT4 = Ep*BB4

Bi4 = cbind(C4,B4)
Bj4 = cbind(BT4,Mab)
A4= rbind(Bi4,Bj4)

Dt4 = det(A4)
A.inv4 = solve(A4)

r4 = matrix(rlnorm(S, 0.9, 1),S,1)
q4 = -matrix(rlnorm(S, 0, 0.1),S,1)
R4  = rbind(r4,q4)

N4 = -A.inv4%*%R4
xx4 = x4
if (length(which(N4<0)) == 0) {
  x4 = -1
}else{
```

```
    x4 = x4+1}

  N.Diag4 = diag(as.numeric(N4))

  AA4 = A4
  #AA4 = N.Diag4%*%A4
}
return(AA4)# return 4




x5=1
while (x5>0) {

  nc = round(ct*S*S, digits = 0)    # Number of connectance species

  B5 = matrix(0,S,S)
  Mab= matrix(0,S,S)


  I <- rep(1,S)
  J <- 1:S
  for(i in 2:(S)){
    I <- c(I,rep(i,S))
    J <- c(J,1:S)
  }


  sam5 <- sample(length(I),nc)
  inter5 <- cbind(I,J)[sam5,]
  for(i in 1:nc){
    if(runif(1) >0.5){
      B5[inter5[i,1],inter5[i,2]]<- -abs(rnorm(1,0,sg))
    }else{
      B5[inter5[i,2],inter5[i,1]]<- -abs(rnorm(1,0,sg))
```

```
    }
  }#B5



  C5 = -diag(runif(S,0.05,1),S,S)
  BB5 = t(abs(B5))
  Ep = matrix(e,S,S)

  BT5 = Ep*BB5

  Bi5 = cbind(C5,B5)
  Bj5 = cbind(BT5,Mab)
  A5= rbind(Bi5,Bj5)

  Dt5 = det(A5)
  A.inv5 = solve(A5)

  r5 = matrix(rlnorm(S, 0.9, 1),S,1)
  q5 = -matrix(rlnorm(S, 0, 0.1),S,1)
  R5  = rbind(r5,q5)

  N5 = -A.inv5%*%R5
  xx5 = x5
  if (length(which(N5<0)) == 0) {
    x5 = -1
  }else{
    x5 = x5+1}

  N.Diag5 = diag(as.numeric(N5))

  AA5 = A5
  #AA5 = N.Diag5%*%A5
}
return(AA5)# return 5
```

```
x6=1
while (x6>0) {

  nc = round(ct*S*S, digits = 0)    # Number of connectance species

  B6 = matrix(0,S,S)
  Mab= matrix(0,S,S)


  I <- rep(1,S)
  J <- 1:S
  for(i in 2:(S)){
    I <- c(I,rep(i,S))
    J <- c(J,1:S)
  }

  sam6 <- sample(length(I),nc)
  inter6 <- cbind(I,J)[sam6,]
  for(i in 1:nc){
    if(runif(1) >0.5){
      B6[inter6[i,1],inter6[i,2]]<- -abs(rnorm(1,0,sg))
    }else{
      B6[inter6[i,2],inter6[i,1]]<- -abs(rnorm(1,0,sg))
    }
  }#B6

  C6 = -diag(runif(S,0.05,1),S,S)
  BB6 = t(abs(B6))
  Ep = matrix(e,S,S)

  BT6 = Ep*BB6

  Bi6 = cbind(C6,B6)
  Bj6 = cbind(BT6,Mab)
  A6 = rbind(Bi6,Bj6)
```

```
  Dt6 = det(A6)
  A.inv6 = solve(A6)

  r6 = matrix(rlnorm(S, 0.9, 1),S,1)
  q6 = -matrix(rlnorm(S, 0, 0.1),S,1)
  R6  = rbind(r6,q6)

  N6 = -A.inv6%*%R6
  xx6 = x6
  if (length(which(N6<0)) == 0) {
    x6 = -1
  }else{
    x6 = x6+1}

  N.Diag6 = diag(as.numeric(N6))

  AA6 = A6
  #AA6 = N.Diag6%*%A6
}
return(AA6)# return 6

x7=1
while (x7>0) {

  nc = round(ct*S*S, digits = 0)    # Number of connectance species

  B7 = matrix(0,S,S)
  Mab= matrix(0,S,S)


  I <- rep(1,S)
  J <- 1:S
  for(i in 2:(S)){
    I <- c(I,rep(i,S))
    J <- c(J,1:S)
  }
```

```
sam7 <- sample(length(I),nc)
inter7 <- cbind(I,J)[sam7,]
for(i in 1:nc){
  if(runif(1) >0.5){
    B7[inter7[i,1],inter7[i,2]]<- -abs(rnorm(1,0,sg))
  }else{
    B7[inter7[i,2],inter7[i,1]]<- -abs(rnorm(1,0,sg))
  }
}#B7

C7 = -diag(runif(S,0.05,1),S,S)
BB7 = t(abs(B7))
Ep = matrix(e,S,S)

BT7 = Ep*BB7

Bi7 = cbind(C7,B7)
Bj7 = cbind(BT7,Mab)
A7= rbind(Bi7,Bj7)

Dt7 = det(A7)
A.inv7 = solve(A7)

r7 = matrix(rlnorm(S, 0.9, 1),S,1)
q7 = -matrix(rlnorm(S, 0, 0.1),S,1)
R7  = rbind(r7,q7)

N7 = -A.inv7%*%R7
xx7 = x7
if (length(which(N7<0)) == 0) {
  x7 = -1
}else{
  x7 = x7+1}
```

```
  N.Diag7 = diag(as.numeric(N7))

  AA7 = A7
  #AA7 = N.Diag7%*%A7
}
return(AA7)# return 7


x8=1
while (x8>0) {

  nc = round(ct*S*S, digits = 0)    # Number of connectance species

  B8 = matrix(0,S,S)
  Mab= matrix(0,S,S)


  I <- rep(1,S)
  J <- 1:S
  for(i in 2:(S)){
    I <- c(I,rep(i,S))
    J <- c(J,1:S)
  }


  sam8 <- sample(length(I),nc)
  inter8 <- cbind(I,J)[sam8,]
  for(i in 1:nc){
    if(runif(1) >0.5){
      B8[inter8[i,1],inter8[i,2]]<- -abs(rnorm(1,0,sg))
    }else{
      B8[inter8[i,2],inter8[i,1]]<- -abs(rnorm(1,0,sg))
    }
  }#B8

  C8 = -diag(runif(S,0.05,1),S,S)
```

```
  BB8 = t(abs(B8))
  Ep = matrix(e,S,S)

  BT8 = Ep*BB8

  Bi8 = cbind(C8,B8)
  Bj8 = cbind(BT8,Mab)
  A8= rbind(Bi8,Bj8)

  Dt8 = det(A8)
  A.inv8 = solve(A8)

  r8 = matrix(rlnorm(S, 0.9, 1),S,1)
  q8 = -matrix(rlnorm(S, 0, 0.1),S,1)
  R8  = rbind(r8,q8)

  N8 = -A.inv8%*%R8
  xx8 = x8
  if (length(which(N8<0)) == 0) {
    x8 = -1
  }else{
    x8 = x8+1}

  N.Diag8 = diag(as.numeric(N8))

  AA8 = A8
  #AA8 = N.Diag8%*%A8
}
return(AA8)# return 8

x9=1
while (x9>0) {

  nc = round(ct*S*S, digits = 0)    # Number of connectance species

  B9 = matrix(0,S,S)
```

```
Mab= matrix(0,S,S)


I <- rep(1,S)
J <- 1:S
for(i in 2:(S)){
  I <- c(I,rep(i,S))
  J <- c(J,1:S)
}


sam9 <- sample(length(I),nc)
inter9 <- cbind(I,J)[sam9,]
for(i in 1:nc){
  if(runif(1) >0.5){
    B9[inter9[i,1],inter9[i,2]]<- -abs(rnorm(1,0,sg))
  }else{
    B9[inter9[i,2],inter9[i,1]]<- -abs(rnorm(1,0,sg))
  }
}#B9

C9 = -diag(runif(S,0.05,1),S,S)
BB9 = t(abs(B9))
Ep = matrix(e,S,S)

BT9 = Ep*BB9

Bi9 = cbind(C9,B9)
Bj9 = cbind(BT9,Mab)
A9= rbind(Bi9,Bj9)

Dt9 = det(A9)
A.inv9 = solve(A9)

r9 = matrix(rlnorm(S, 0.9, 1),S,1)
q9 = -matrix(rlnorm(S, 0, 0.1),S,1)
```

```
  R9  = rbind(r9,q9)

  N9 = -A.inv9%*%R9
  xx9 = x9
  if (length(which(N9<0)) == 0) {
    x9 = -1
  }else{
    x9 = x9+1}

  N.Diag9 = diag(as.numeric(N9))

  AA9 = A9
  #AA9 = N.Diag9%*%A9
}
return(AA9)# return 9

x10=1
while (x10>0) {

  nc = round(ct*S*S, digits = 0)    # Number of connectance species

  B10 = matrix(0,S,S)
  Mab= matrix(0,S,S)


  I <- rep(1,S)
  J <- 1:S
  for(i in 2:(S)){
    I <- c(I,rep(i,S))
    J <- c(J,1:S)
  }

  sam10 <- sample(length(I),nc)
  inter10 <- cbind(I,J)[sam10,]
  for(i in 1:nc){
    if(runif(1) >0.5){
```

```
      B10[inter10[i,1],inter10[i,2]]<- -abs(rnorm(1,0,sg))
    }else{
      B10[inter10[i,2],inter10[i,1]]<- -abs(rnorm(1,0,sg))
    }
  }#B10

  C10 = -diag(runif(S,0.05,1),S,S)
  BB10 = t(abs(B10))
  Ep = matrix(e,S,S)

  BT10 = Ep*BB10

  Bi10 = cbind(C10,B10)
  Bj10 = cbind(BT10,Mab)
  A10= rbind(Bi10,Bj10)

  Dt10 = det(A10)
  A.inv10 = solve(A10)

  r10 = matrix(rlnorm(S, 0.9, 1),S,1)
  q10 = -matrix(rlnorm(S, 0, 0.1),S,1)
  R10  = rbind(r10,q10)

  N10 = -A.inv10%*%R10
  xx10 = x10
  if (length(which(N10<0)) == 0) {
    x10 = -1
  }else{
    x10 = x10+1}

  N.Diag10 = diag(as.numeric(N10))

  AA10 = A10
  #AA10 = N.Diag10%*%A10
}
return(AA10)# return 10
```

```
M01 = cbind(Mab,Mab)
M02 = cbind(Mab,Mab)
M0  = rbind(M01,M02)


J1 = cbind(AA1,M0,M0,M0,M0,M0,M0,M0,M0,M0)
J2 = cbind(M0,AA2,M0,M0,M0,M0,M0,M0,M0,M0)
J3 = cbind(M0,M0,AA3,M0,M0,M0,M0,M0,M0,M0)
J4 = cbind(M0,M0,M0,AA4,M0,M0,M0,M0,M0,M0)
J5 = cbind(M0,M0,M0,M0,AA5,M0,M0,M0,M0,M0)
J6 = cbind(M0,M0,M0,M0,M0,AA6,M0,M0,M0,M0)
J7 = cbind(M0,M0,M0,M0,M0,M0,AA7,M0,M0,M0)
J8 = cbind(M0,M0,M0,M0,M0,M0,M0,AA8,M0,M0)
J9 = cbind(M0,M0,M0,M0,M0,M0,M0,M0,AA9,M0)
J10= cbind(M0,M0,M0,M0,M0,M0,M0,M0,M0,AA10)


Diag.NA = rbind(J1,J2,J3,J4,J5,J6,J7,J8,J9,J10)

dab1 = diag(d1/(n-1),S,S)   # Diagonal matrix of d1/n-1 for host
dab2 = diag(d2/(n-1),S,S)   # Diagonal matrix of d2/n-1 for parasite

da1 = cbind(dab1,Mab)
db1 = cbind(Mab,dab2)
DP  = rbind(da1,db1)

D11 = diag(-d1,S,S)         # Diagonal matrix of -d1 for host
D12 = diag(-d2,S,S)         # Diagonal matrix of -d2 for parasite

Da1 = cbind(D11,Mab)
Db1 = cbind(Mab,D12)
Dab = rbind(Da1,Db1)


D1 = cbind(Dab,DP,DP,DP,DP,DP,DP,DP,DP,DP)
```

```
  D2 = cbind(DP,Dab,DP,DP,DP,DP,DP,DP,DP,DP)
  D3 = cbind(DP,DP,Dab,DP,DP,DP,DP,DP,DP,DP)
  D4 = cbind(DP,DP,DP,Dab,DP,DP,DP,DP,DP,DP)
  D5 = cbind(DP,DP,DP,DP,Dab,DP,DP,DP,DP,DP)
  D6 = cbind(DP,DP,DP,DP,DP,Dab,DP,DP,DP,DP)
  D7 = cbind(DP,DP,DP,DP,DP,DP,Dab,DP,DP,DP)
  D8 = cbind(DP,DP,DP,DP,DP,DP,DP,Dab,DP,DP)
  D9 = cbind(DP,DP,DP,DP,DP,DP,DP,DP,Dab,DP)
  D10= cbind(DP,DP,DP,DP,DP,DP,DP,DP,DP,Dab)

  D   = rbind(D1,D2,D3,D4,D5,D6,D7,D8,D9,D10)

  AA = Diag.NA + D
}

# Parameters

sg = 1                # Interspecific interaction strength
ct = 1                # Connectance
S  = 5                # Number of species
e  = 0.5              # Coefficient efficiency
d1 = 8                # Dispersal rate for host
d2 = 8                # Dispersal rate for parasite
n  = 10               # Number of patches

AA = Bipartite_Generator(S,ct,sg,e,d1,d2,n)

E = eigen(AA)$values

pdf("biNC5.pdf",3,4)
plot(Re(E), Im(E), pch=20, xlim = c(-10,0), ylim = c(-5,5),
     xlab = "Real", ylab = "Imaginary", main = "e",cex.main=2,cex.lab=1,cex.axis=
abline(h=0, lty=1)
abline(v=0, lty=1)
dev.off()
```

```
# R code for numeral simulations for both predator-prey and bipartite

Diffusion.rate = seq(1e-04,1e+02)  # Diffusion rate
Res = c()

for(i in 1:length(Diffusion.rate)){
  d = Diffusion.rate[i]
  Largest.real.part = c()
  for (j in 1:100) {
    AA = H_P_meta_community(S,C,sg,m,e,d,n)
    E = eigen(AA)$values
    Jacobian = max(Re(E))
    Largest.real.part = append(Largest.real.part,Jacobian)
  }
  mean(Largest.real.part)
  Res = append(Res, mean(Largest.real.part))
}

plot(Diffusion.rate, Res, "l", xlab = "Diffusion rate",
 ylab = "Largest real part", main = "b",cex.main=4,cex.lab=2,cex.axis=2)
```